RECENT ADVANCES

IN

THE PHYSIOLOGY OF MOTION,

THE

SENSES, GENERATION, AND DEVELOPMENT.

BY WILLIAM BALY, M.D., F.R.S.,

PHYSICIAN TO MILLBANK PRISON, AND LECTURER ON FORENSIC MEDICINE AT ST. BARTHOLOMEW'S HOSPITAL;

AND

WILLIAM SENHOUSE KIRKES, M.D.

BEING A

SUPPLEMENT TO THE SECOND VOLUME

OF

PROFESSOR MÜLLER'S "ELEMENTS OF PHYSIOLOGY."

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PREFACE.

At an early period after the publication of the last part of the English edition of Professor Müller's Physiology, it became necessary to reprint the second volume of the work; a second edition of the first volume having already been issued. The second volume did not then need complete revision and re-editing; it was therefore reprinted with only a few verbal alterations. But it was determined that, after a certain lapse of time, there should follow a Supplement or Appendix, containing later information on the subjects treated of in the most important portion of the volume, namely, that portion comprising the Physiology of Generation and Development; and reference was made to such an Appendix in several pages of the reprinted volume.

In accordance with this plan, I was occupied during part of the winter of 1845-6, with preparing an account of the advances made in the course of the previous three years in the departments of science just named, but other unavoidable engagements interrupted my progress with the undertaking at that time, and subsequently prevented me from resuming it. The project, however, could not well be relinquished. Finding, therefore, a few months since, that I still was not able to command the requisite leisure, I proposed to Messrs. Taylor and Walton that Dr. Kirkes should be requested to lend his aid towards the immediate completion of the work, a proposal to which they readily acceded. And Dr. Kirkes very kindly consented to render the assistance required, although himself engaged in the preparation of a separate Treatise on Physiology.

It has been found advisable to extend the original plan of the present work, and to make it supplementary to the entire second volume of Professor Müller's Elements of Physiology, by including an account of the more important advances in the Physiology of Motion and of the Senses. These departments of the science have not, however, been so

actively cultivated during the last few years, and are not so extensive in their scope as those of Generation and Development. A larger space has, therefore, been devoted to the latter, than to the former subjects. To the Physiology of the Mind, for reasons which it is unnecessary to explain, no additions have been made.

It remains only to state that the portion of this work, comprehending the following subjects:—"The Unimpregnated Ovum," "the Semen," "the Discharge of Ova from the Ovaries," "the Nature and Purport of the Corpus Luteum," "Menstruation," and "the Changes which take place in the Impregnated Ovum, down to the completion of the Cleaving-process," has been written by myself, the greater part of it during the winter of the years 1845-6; that the remainder has been written by Dr. Kirkes, and that the whole has been prepared for the press by Dr. Kirkes and myself conjointly.

WILLIAM BALY.

28, Spring Gardens,
27th March, 1848.

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ERRATA.

PAGE

52. The title of M. Zwicky's dissertation on the corpus luteum, which has been accidentally omitted, is "De Corporum Luteorum Origine atque Transformatione. Diss. Inaug. by H. L. Zwicky, Turici, 1844."

99, 8 lines from the bottom, *instead* of "M. Dumesny," *read* "M. Duvernoy;" and in the *note* corresponding to this, *after* "1844," *read* "Zoologie, tome i."

112, *note, after* "Menschlichen," *read* "Körpers."

125, 11 lines from the bottom, *instead* of "variety," *read* "rarity."

RECENT ADVANCES

IN THE

PHYSIOLOGY OF MOTION IN ANIMALS.

OF CILIARY MOTION.*

Some additional information has been obtained with regard to the *parts occupied by ciliary epithelium* in the human subject, and in mammalia generally. It is found,† for example, that this variety of epithelium, besides lining the interior of the nasal cavity, and of the frontal and maxillary sinuses communicating with this cavity, is continued up the lachrymal canal into the lachrymal sac, and is also spread over the mucous surface of both eyelids, but not over the conjunctiva covering the eye itself. From the posterior part of the nasal cavity, the ciliary epithelium passes to the upper part of the pharynx, which it lines to about opposite the lower border of the atlas: it is also spread over the posterior surface of the root of the soft palate, and laterally it is continued to the orifice of the Eustachian tube, up which canal it extends into the cavity of the tympanum.

It was until recently believed that the ciliary motion is entirely wanting in the urinary apparatus of Vertebrata. But it has been found by Mr. Bowman,‡ that in frogs a layer of ciliary epithelium lines the urinary tubules just at their junction with the Malpighian capsules; and this observation has been verified by Bischoff,§ Valentin,‖ and others. Valentin was able to trace the ciliary motion even within the Malpighian capsules; so also was Pappenheim. In the kidneys of lizards, Kölliker ¶ states he has observed ciliary movements along the entire length of the urinary tubules, except at their exit from the gland, and just where they dilate into their terminal extremities within the substance of the organ. No

* Vide Book iv. section 1, Chapter ii. p. 853, of Professor Müller's Elements of Physiology.

† Vide Henle's Allgemeine Anatomie, p. 246 *et seq.* for the best recent account of the localities of ciliary epithelium.

‡ Philosophical Transactions, 1842.

§ Müller's Archiv. 1843, p. 132.

‖ Repertorium, b. viii. p. 92.

¶ Müller's Archiv. 1845, p. 519.

trace of cilia has yet been found in any part of the urinary apparatus of Mammalia.

M. Rossignol* finds that the ciliary epithelium along the mucous lining of the respiratory passages, ceases at the vesicular structure of the lung, its place in the vesicles themselves being occupied by simple pavement epithelium, composed of roundish or oval cells. The cessation of the ciliary epithelium at the commencement of the cellular structure of the lung, has been observed also by Mr. Rainey, † who states, however, that the intercellular passages and the air-vesicles in which the ultimate branches of the bronchial tubes terminate, are destitute of epithelium of any kind.

Ecker ‡ has discovered ciliary epithelium in the semi-circular canals of the internal ear of Petromyzon marinus (sea lamprey). The cells were of different forms, oval, roundish, flask-shaped, and angular, with nuclei and granular contents. None of the cells possessed more than one cilium. The movements of the cilia were principally of a lashing, fanning kind. This is the first example of a ciliary structure being found in any other part of the auditory apparatus of a vertebrate animal, than the Eustachian tube.

Of the phenomena of ciliary motion.—An interesting observation in regard to the mode of action of the cilia, has been made by Mr. Quekett§ in the case of the gill rays of the mussel, which explains more completely than could otherwise be done, the power possessed by the cilia of propelling fluid or solid particles in any determinate direction. He observed, that besides their ordinary lashing movements, each cilium possesses a kind of rotatory motion on itself, by which it turns on its own axis, through the space of about a quarter of a circle, with a movement very similar to that performed during the *feathering* of an oar in rowing.

Nature of the ciliary motion.—From experiments made on the epithelial cells of the nasal mucous membrane of man, E. H. Weber|| has shewn that the vibratile movements of their cilia are diminished almost to one-half their usual rate by cold, and are sensibly increased by heat. In this as well as in their rhythmic action and its persistence after death, the ciliary movements bear a close analogy to those of the heart. The influence of heat and cold is less manifest on the movements of the cilia, and also on those of the heart, in cold than in warm-blooded animals.

OF THE MUSCULAR AND THE ALLIED MOTIONS.¶

Of the elastic and contractile tissue of arteries.

THE statement made by Professor Müller,** that the middle coat of arteries does not possess any muscular contractility, requires to be

* Recherches sur la Struct. du Poumon. Bruxelles, p. 66—8.

† Medico-Chirurg. Transact. vol. xxviii.

‡ Müller's Archiv. 1844, p. 520.

§ Medical Gazette, May 3, 1844.

|| Archiv. d'Anat. Gen. et de Physiol. Jan. 1846.

¶ Chapter iii. p. 867, Müller's Physiology.

** Physiology, p. 875.

somewhat modified, principally on account of the investigations of Henle,* which have shewn that besides elastic tissue, the middle arterial coat is provided with fibres in all respects analogous to those of organic muscle.

This discovery is one of considerable importance, because it serves to explain what was hitherto unintelligible, the well-known property possessed by arteries, especially by the smaller ones, of contracting, under certain circumstances, to a diameter smaller than that which their elasticity alone could enable them to assume. Although this property has been matter of almost universal observation, yet by few writers has any plausible explanation of it been suggested. The sagacity of John Hunter, unaided by microscopic evidence, led him to conclude that the contraction of arteries was really a muscular act.† Yet this opinion appears to have been lost sight of, for most writers since Hunter's time, including Professor Müller, have attributed the contraction of the arterial coats to a peculiar vital property, to which they gave the name of tonicity or insensible contractility, without being able to refer this property to any definite structure. In the last German edition of the first volume of his work,‡ Professor Müller alludes to this discovery by Henle, and considers it probable that the fibres described by him are the seat of the contractile power of the arteries, though he appears disinclined to admit their muscular nature.

Chemical evidence also in favour of Henle's account has been procured by Dr. Retzius,§ who finds that a solution of the arterial coat in acetic acid is precipitated by cyanide of potassium; this shews that some elements besides cellular and elastic tissues enter into its composition, for the solution in acetic acid of neither of these tissues is precipitated by cyanide of potassium. And that organic muscular fibre constitutes one of these other elements has, since then, been rendered tolerably certain by Dr. F. C. Donders,|| who, by acting upon the middle arterial coat of young sheep with a solution of potash, observed that in two or three hours the fibres of this coat separated from each other, became granular and then dissolved; changes exactly similar to those which he found organic muscular fibres, under like circumstances, to undergo. The existence of muscular fibres in the middle arterial coat is also inferred by the same physiologist ¶ from the effects produced upon it by the action of nitric acid and ammonia. When strong nitric acid is applied to a protein-compound, it forms with

* Casper's Wochenschr. May 28, 1840; and Allgem. Anat. 1842, p. 498.

† Works, Palmer's edition, vol. iii. pp. 156—71, comprising his account of the structure of arteries, where (as Mr. Paget has pointed out) abundant proofs are given by Hunter of the existence of muscular power, especially in the smaller arterial branches.

‡ 1841, page 171.

§ Physiol. des Mensch. by Prof. J. Müller, Coblenz. Fourth edition. Vol. i. p. 171.

|| Holländische Beiträge zu den Anat. und Physiol. Wissenschaften, 1846, p. 55.

¶ Op. cit. p. 67.

it what is termed, xantho-proteinic acid, which, with ammonia, produces a yellow xantho-proteinate of ammonia. On applying this test, with the requisite cautions, to the coats of blood-vessels, Dr. Donders found that the middle arterial coat alone assumed the characteristic yellow colour. The other coats, as well as all the coats of veins, remained unchanged in colour.

But the most satisfactory evidence is that furnished by some recent experiments of Ed. and E. H. Weber,* in which they applied the stimulus of electro-magnetism to small arteries. One principal circumstance which induced Professor Müller to deny the muscularity of arteries, was the inability of himself, and of other experimenters who had occupied themselves on the subject, to produce the slightest movements in arteries by means of galvanic and electric stimuli, while in all true muscular tissues these stimuli give rise to manifest contractions. An explanation of the failure of these physiologists, may be found in the circumstance that in nearly all their experiments, the arteries examined were of large size, such as the aorta and the carotids, in which the thickness of the muscular coat is comparatively small. The experiments of the Webers were, on the other hand, performed on the small mesenteric arteries of frogs; and the most striking results were obtained, when the diameter of the vessels examined did not exceed from $\frac{1}{7}$ to $\frac{1}{17}$ of a Paris line. When a vessel of this size was exposed to the electric stream, its diameter, in from five to ten seconds, became one-third less, and the area of its section about one-half. On continuing the stimulus, the narrowing gradually increased, until the calibre of the tube became from three to six times smaller than it was at first, so that only a single row of blood-corpuscles could pass along it at once; and eventually the vessel became completely closed and the current of blood arrested. When the experiment was so conducted, that only a limited part of an artery was exposed to the electric stream, the extent of tube involved in the contraction was equally limited, not exceeding from $\frac{1}{8}$ of a line to a line. The contraction did not ensue the moment the irritation was applied, and it continued for a short time after its withdrawal. The walls of the artery were rendered somewhat thicker at the contracted part, but the narrowing of the canal was proportionally greater than the increase in thickness acquired by the walls. Previous to the complete closure of the artery, the velocity of the stream of blood passing through it, in accordance with hydraulic principles, became considerably accelerated. When an artery was irritated only for a short time, or by a feeble galvanic current, it speedily resumed its former calibre on the stimulus being withdrawn, and again contracted on a re-application of it; but when the irritation was long continued, or the stream very powerful, the portion of the artery narrowed by it lost the power of again contracting, and even dilated, until it became double

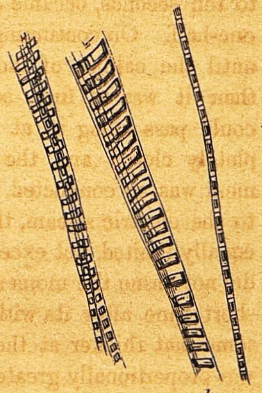
* Müller's Archiv. 1847, p. 232, *et seq.*

its former size, forming a kind of aneurism on the trunk of the vessel. When the abdominal aorta and other large arteries were experimented on in the above manner, no decided appearance of contraction ensued; a result agreeing with the observations of the experimenters before alluded to. The electric current produced no contraction of the capillaries, and only a slight one of the small mesenteric veins. One other remarkable circumstance observed in the Webers' experiments may, though out of place, be here mentioned, on account of its novelty and importance; and that is, the speedy arrest and subsequent coagulation of the blood in the vessels, especially the capillaries, exposed to the influence of the electro-magnetic stream. The blood corpuscles adhered unusually to each other and to the walls of the vessels, and by the greater amount of friction thus produced, they became retarded in their onward movement and eventually arrested.

Of the muscular tissue.

Structure of muscle.—Recent microscopic examination of muscles of animal life, appears to have thrown further light on the structure of the ultimate fibrils.* It is found that, with an instrument of good defining power, the border of each fibril appears straight, or nearly so, and that the alternate dark and light particles of which the fibril is composed, have each a quadrilateral and generally a rectangular form. It is found, also, that every bright particle or space is marked across its centre by a fine, dark, tranverse line or shadow, by which the space is divided into two equal parts, and that, "sometimes, also, a bright border may be perceived on either side of the fibril, so that each of the rectangular dark bodies appears then to be surrounded with a bright area, having a similar quadrangular outline, as represented in the figure annexed, and it may therefore be inferred that the pellucid substance incloses it on all sides. In short, it would seem that the elementary particles of which the fibril is made up,

Fig. 1.†



* Dr. Sharpey, in the Fifth Edition of Quain's Anatomy; and Dr. Carpenter in his Manual of Physiology, 1846.

† Fig. 1. "Muscular fibrillæ of the pig, magnified 720 diameters. *a.* An apparently single fibril, shewing the quadrangular outline of the component particles, their dark central part and bright margin, and their lines of junction crossing the light intervals. *b.* A longitudinal segment of a fibre consisting of a number of fibrils still connected together. The dark cross stripes and light intervals on *b* are obviously occasioned by the dark specks and intervening light spaces respectively corresponding in the different fibrils. *c.* Other smaller collections of fibrillæ. From a preparation by Mr. Lealand." After Dr. Sharpey.

are little masses of pellucid substance presenting a rectangular outline, and appearing dark in the centre. Their appearance, indeed, suggests the notion of minute vesicular bodies or cells, cohering in a linear series, the faint transverse marks between being the lines of junction." * On altering the focus, however, the dark spot, as Dr. Sharpey continues to observe, becomes light and appears transparent, though less so than the bright marginal portion. Moreover, when very highly magnified, the dark central part also appears, according to the same observer, marked or constricted in the middle, as if consisting of two separate particles. Whether, therefore, the appearances above described depend on each pellucid particle being really a nucleated cell, and whether the ultimate fibril is to be considered as composed of a single row of such cells opposed end to end, by whose closer approximation to each other the contraction of the fibril is effected, are questions not yet determined.

After repeated examinations of transverse sections of striped muscular fibre, M. Stadelmann † has convinced himself that (as was stated by Mr. Bowman) ‡ the tube of the primitive fibre is invariably filled throughout with fibrillæ, and never presents the central cavity described by some writers. A slight appearance of the existence of such cavity is frequently afforded by the dots, which indicate the cut fibrillæ, being much paler at the centre of the fibre than towards its circumference, but they are never so pale as to be invisible.

Cause of the striped appearance of animal muscular fibre.—In addition to the several arguments employed by Professor Müller,§ in favour of the opinion that the tranversely striated appearance of voluntary muscular fibre is due to the peculiar structure of the ultimate fibrils of which the fibre is composed, and not to markings on the sheath of the fibre, Mr. Bowman draws attention to another conclusive circumstance, namely, that by successively bringing into focus fresh portions of the depth of a fibre, the first observed striæ become confused, or even vanish, whilst others come into view; shewing that they exist not merely on the surface, but through the entire thickness of the transparent fibres. ||

Relative size of the fibres and fibrils of striped muscle in the fœtus and adult.—The correctness of Mr. Skey's statement,¶ that the primitive fibres of voluntary muscle in the fœtus have a diameter about one-third of that which they possess in adult age, has been recently shewn

* Dr. Sharpey, l. c. p. clxviii.

† Reichert's Bericht in Müller's Archiv. 1845, p. 192.

‡ Philosoph. Trans. 1840, p. 467. § Müller's Physiology, p. 880.

|| Philosophical Transactions, 1840, p. 468. The two Webers remain the strongest upholders of the opinion that the transverse markings of the fibres are seated in the sheath; but since their evidence in favour of this view is by no means conclusive, it is not necessary to do more than refer to the article "Muskelbewegung" in Wagner's Handwörterbuch, by Professor Ed. Weber. ¶ Müller's Physiology, p. 881.

by Professor Harting,* who observes that the average diameter of the fibres in the new-born child is to that in the adult as 1:3·64, and that the respective average intervals between the transverse striæ are as 1:1·18. He finds, also, that in the child the distance between the striæ is to the width of the fibre as 1:4·415; in the adult as 1:8·42.

Attachment of muscle to tendon.—Mr. Paget † has recently discovered a new mode of attachment of the ultimate fibres of muscle to their tendons: it was observed in the muscle torn out from the leg of a fly. "Each of three tendons, which are planted in the proximal end of the last but one articulation of the leg, runs in a long, straight, and flat band up the interior of the next superior division of the limb, and receives on each of its edges the broad and somewhat rounded bases of the muscular fibres. These are arranged in a penniform manner, the base of each fibre on one side of the tendon corresponding to the halves of the bases of two adjacent fibres on the opposite side, like the leaflets of the Pteris and some other ferns. The fibres are flat, and their extremities, instead of being ensheathed in the tendinous tissue, only adhere to the border of the tendon, and receive on their outer edges one or two finer tendinous filaments, as if for greater fixity."

Involuntary muscles which are composed of striped fibres.—In addition to the heart, which is the only involuntary muscular organ mentioned by Professor Müller,‡ as having the striped or beaded variety of muscular fibre in its composition, must now be enumerated the lymphatic hearts of reptiles and birds; § the coats of the stomach and intestines of the tench, and of the stomach in the common roach.||

Of the vital properties of muscle.

The apparent hardness of muscles in the state of contraction has been shewn by Professor Ed. Weber ¶ to be caused by the tension which their fibres, as well as their tendons and other tissues, are subjected to from the resistance ordinarily opposed to their contraction. For, when no resistance is offered, as when a muscle is cut off from its tendon, no hardness is perceptible during contraction; indeed, he finds that the muscular tissue is then even softer, more extensile, and less elastic than in its uncontracted state.

Changes in muscle during its contraction.—From what has been learned of late concerning the minute anatomy of striped muscular fibre, and from

* Tijdschr. Voor Natur. Geschied. en Physiol. d. xii. quoted in Mr. Paget's Report on Physiology in 1844–5, p. 11.

† Report on Anatomy and Physiology for 1842–3, p. 6.

‡ Physiology, p. 879.

§ Prof. Stannius in Müller's Archiv. 1843.

|| Prof. Budge, Schmidt's Jahrb. 4, 1847.

¶ Loc. Cit. Art. Muskelbewegung, p. 54.

peculiarities observed in its mode of action, it appears probable that the contraction of this kind of muscle, is effected in all cases simply by a closer approximation of the constituent parts of the primitive fibrils without any change taking place in their general direction, — without the production of any zig-zag inflexions. In addition to the several reasons stated by Professor Müller,* for considering this approximation of particles, as at least one of the modes in which the fibres become shortened, must be mentioned the conclusive observations of Mr. Bowman,† and Professor Ed. Weber,‡ both of whom have examined muscular fibre during its state of contraction. Mr. Bowman's observations were chiefly made on the fibre of muscles which were spontaneously passing into the state of rigor mortis. He noticed that at the contracted part of the fibre, the transverse striæ were approximated closer to each other than elsewhere, and gave to the fibre at such parts a somewhat darker appearance than was presented by the uncontracted portions. Professor Ed. Weber's observations were made on muscular fibres while contracting under the influence of an electric current from a rotatory magnet. He states that, under such circumstances, the contraction may be observed to be attended by a simple shortening and thickening of the individual fibres; and that in this shortening, every part of the contracting fibre participates, so that the outline of the fibre remains uniformly straight, and presents no appearance either of zig-zag inflexions or of the beaded or knotted characters described by Mr. Bowman. The zig-zag inflexions, however, are produced immediately on the cessation of the contraction, and result, as shewn also by Mr. Bowman, from the resistance which the fibres meet, in their endeavour to elongate to their former state, during relaxation. In the case of individual fibres beneath the microscope, this resistance is caused by friction on the surface of the glass. In other cases it probably results from the fibre, though itself relaxed, being prevented from elongating, and its ends thus kept approximated, by the contraction of neighbouring fibres, or by its not being stretched by the action of antagonist fibres. Any of these circumstances would be sufficient to produce the wavy zig-zag appearance frequently observed: and, it may now be considered as tolerably certain, that such an appearance indicates, as Professor Owen and Dr. Allen Thomson originally supposed, that the fibre is in a state of relaxation, and it may likewise be assumed that in all cases the contraction of muscle is effected by the closer approximation of its component particles without the fibres themselves being thrown out of the straight line. It should be stated, however, that Valentin § continues opposed to this view, and still considers the contraction to be attended by the production of zig-zag flexures.

* Physiology, p. 889. † Philosophical Transactions, 1840.
‡ Archives d'Anat. Gen. et de Phys. Janvier, 1846.
§ Lehrbuch der Physiol. des Menschen, b. ii. p. 33.

The rigidity of muscles after death.—Much has been written of late on the subject of the post-mortem rigidity of muscles, though in addition to what was stated by Professor Müller,* few new facts of importance have been obtained, beyond some which tend to confirm the general opinion, that the rigidity is dependent upon an actual contraction of the muscular tissue,† and that it does not occur until the muscles have lost their irritability, or their power of contracting on the application of ordinary stimuli. Among other facts in proof of the latter of these circumstances, it has been observed by Dr. Gierlichs,‡ that in frogs, in whom, as in other reptiles, the muscular irritability is very persistent, the rigor mortis is often not established for three or four days after death; that in birds, on the other hand, whose muscular irritability endures but a short time after death, the post-mortem rigidity ensues quickly. Additional proof also has been procured, both by Dr. Gierlichs and other observers, that all circumstances which cause a speedy exhaustion of muscular irritability, induce an early occurrence of the cadaveric rigidity, while conditions by which the disappearance of the irritability is delayed, are succeeded by a tardy onset of this rigidity.

The rigidity of voluntary muscles, from being the most evident, has attracted most attention, and the phenomenon has, until lately, been described solely in relation to this class of muscles, but sufficient evidence has now been accumulated to warrant the conclusion, that the involuntary muscles also are affected by a post-mortem rigidity, which is, in all essential respects, comparable with that seated in the voluntary muscles. And this is true, not merely with regard to those involuntary muscles which, such as the blood and lymphatic hearts, are constructed of striped fibres, but also with regard to the tissues composed of unstriped fibres, such as the muscular coat of the intestines, and the contractile coat of blood-vessels and of the large excretory ducts. The observations of Dr. George Budd § and of Mr. Paget,|| have proved this in the case of the heart; and the occurrence of the rigidity in the digestive canal has been shewn by Valentin,¶ who found that if a graduated tube be connected with a portion of intestine taken from a recently slain animal, filled with water and tied at the opposite end, the water will in a few hours rise to a considerable height in the tube, owing to the contraction of the intestinal walls. The contraction of the blood-vessels after death was observed by John Hunter, and is now regarded as a well established fact, and one by which the empty state of the arterial system after death is in great measure explained.

* Physiology, p. 890, *et seq.*

† See especially Mr. Bowman in the Philosophical Transactions, 1840; and M. Bruch in Gazette Médicale de Paris, Novembre 1, 1845.

‡ Schmidt's Jahrbuch. Mai, 1844.

§ Medico-Chirurg. Trans. vol. xxi. p. 296.

|| Report on the Progress of Anat. Physiol. 1842–3, p. 6.

¶ Physiologie, b. ii. p. 36.

Are the nerves the sole conductors through the medium of which all stimuli necessarily act on the muscles? *—Some singular results obtained by Dr. E. Harless,† from experiments undertaken for the purpose of determining the relation in which the nervous influence stands towards the irritability of muscular tissue, will, if confirmed, throw doubt on the truth of Müller's opinion that the functional integrity of the nerves ramifying in the muscles is necessary for the excitement of muscular contractions, and that the muscles themselves are not susceptible of the direct action of stimuli. Having exposed rabbits to the influence of the vapour of ether, until they were so far overpowered by it that no movements of their bodies could be excited by means even of galvanism, they were killed by opening the carotid arteries, and the brain and spinal cord exposed. On galvanizing these nervous centres not the slightest movement of the body resulted, but when the galvanic stimulus was applied to the muscles of the trunk, violent contractions at once ensued. Galvanizing the crural nerve produced not the slightest action of the muscles of the corresponding leg, but these muscles were thrown into immediate contraction when the stimulus was applied directly to themselves. Similar results were obtained by galvanizing the nerves and then the muscles of other parts of the body. The result in all cases appeared to point to the conclusion that the muscular tissue possesses within itself an inherent power of contraction, independent of the influence of the nerves distributed to it; for, in these experiments, the nervous system was so far overpowered by the ether, that no amount of irritation of it could excite muscular contractions, while these contractions were at once induced when the irritation was applied to the muscular tissue itself.

* Müller's Physiology, p. 898.

† Müller's Archiv. 1847, p. 228.

VOICE AND SPEECH.*

Very little new information has been contributed to this department of physiology, since the period at which the second volume of Professor Müller's Elements of Physiology was published in this country. A more extended and detailed account of his experiments on the production of the voice, than was contained in the body of his work, has indeed been furnished by Professor Müller† himself, but these details are chiefly explanatory and confirmatory of his former views.

It may be desirable to make some allusion to a highly-ingenious piece of mechanism constructed by M. Faber, a German, and exhibited in this country about two years ago. By means of this curious apparatus, which appears to be by far the most perfect speaking machine yet invented, the peculiarities of the human voice in speaking, singing, and whispering, are very closely imitated. The various difficulties involved in the construction of such an apparatus appear to have entailed many years of close labour upon the inventor; but, as yet, he has not published any account of the methods by which he has so successfully overcome these difficulties.‡

Ventriloquism.—The general correctness of Professor Müller's account of the probable mode of production of this peculiarity of the human voice,§ has been confirmed by M. Colombat,|| who states that by continually practising, in a manner somewhat similar to that pointed out by Professor Müller, he was enabled to attain considerable skill in the production of this variety of voice. The essential mechanical parts of the process consist in taking a full inspiration, then keeping the muscles of the chest and neck fixed, and speaking with the mouth almost closed, and the lips and lower jaw as motionless as possible, while air is very slowly expired through a very narrow glottis; care being taken also, that none of the expired air passes through the nose. But, as observed by Professor Müller, much of the ventriloquist's skill consists in deceiving other senses than hearing.

Falsetto notes.—Professor Müller's explanation of the probable mode of production of falsetto notes has been questioned by MM. Pétrequin and

* Section iii. chap. i. p. 972, Müller's Physiology.

† Ueber Compensation. der phys. Kräfte am Menschl. Organ. Berlin. 1839.

‡ About six years ago, indeed, a description of this apparatus, as far as it was then contrived, was given by Dr. E. Schmulz. (Casper's Wochenschrift, 1842, p. 785.) But at that period M. Faber does not appear to have brought it to the state of perfection it has now attained. The essential parts concerned in the production of speech, such as the vocal cords, the tongue, and the walls of the mouth and nose are said to be formed of caoutchouc.

§ Physiology, p. 1054.

|| Frorieps N. Notizen, 1840, No. 290, s. 55.

Diday * who offer an entirely different account of the cause of these notes from any yet published. According to Professor Müller's account,† the falsetto notes are produced by the vibration only of the inner borders of the vocal cords, while in the production of the natural notes, the entire thickness of the cords is thrown into vibration. In the opinion of Pétrequin and Diday, however, the falsetto notes do not result from the vibrations of the vocal cords at all, but merely from those of the air passing through the aperture between the vocal cords, which, during their production, they suppose to assume the contour of the embouchure of a flute. Their arguments in favour of this opinion are founded almost entirely upon peculiarities observed during the production of the falsetto voice. They remark, for example, that it is very common for high-chest notes to pass into the corresponding falsetto notes, if the singer tries to soften them; for at such times the glottis is instinctively constricted to prevent the note from falling, in consequence of the diminished force of the current of air; and if under these circumstances, the vocal cords are rendered more tense in order to the production of a still higher note, the current of air is unable to make them vibrate, but vibrates itself as it passes through the glottis, and a falsetto note is thus produced—the glottis changing from a reed-like to a flute-like instrument. So also in trying to strengthen a low falsetto note it almost invariably becomes a chest note, on account of the vocal cords passing from a rigid to a vibrating state, while the air itself, which is impelled through the glottis, ceases to vibrate. In illustration of their view, they also state, that if while blowing a reed-instrument, such as a bassoon, the reed is taken hold of and held with forceps so as to prevent it from vibrating, its notes—which before resembled chest-notes—assume at once the falsetto character; becoming acute, soft, and whistling.

M. Cogniard Latour ‡ has drawn attention to the circumstance that in tongued instruments the number of vibrations, and consequently the height of the tone, is dependent on the weight or other peculiarities of the tongue. He found, for example, that under exactly similar circumstances a tongue of brass vibrated 200 times, a tongue of wood 314 times, and a tongue of elder pith 800 times. Reasoning from this, he believes that in persons with deep voices the vocal chords will be thicker and heavier than in other individuals; and that the deep tone or hoarseness of the voice during a catarrh is owing to the chords being swollen. From experiments with double-tongued instruments he also concludes that the walls of the larynx, as well as the vocal chords, take part in the production of the tones of the voice; and he believes that the small and weak voice of old people is to be ascribed to the inelastic, more or less ossified, condition of the larynx.

* Gazette Médicale, 1844. † Physiology, p. 1013.

‡ Canstatts Jahresbericht, Physiologie, 1845, p. 207.

RECENT ADVANCES

IN THE

PHYSIOLOGY OF THE SENSES.

OF THE SENSES GENERALLY.*

Influence of cold and heat on the nerves of sense.—It appears, from some ingenious experiments by Professor E. H. Weber,† that the prolonged application of either heat or cold to nerves of ordinary or special sensation diminishes, or suspends for a time, their power of conveying to the sensorium the effects of impressions made on them. Professor Weber found, for example, that on keeping the tongue immersed for from half a minute to a minute in water heated to about 125° Fahr., and then bringing it in contact with sugar, in powder or in solution, the sweet taste of the sugar was no longer perceived. Moreover, the sense of touch, usually so delicate at the tip of the tongue, was also rendered imperfect. A sensation of numbness was induced in the organ, not unlike that perceived in a limb when "asleep;" and this sometimes remained for about six seconds, or longer. A similar imperfection of taste and touch was produced by immersing the tongue for the same length of time in a mixture of water and broken ice. The cold as well as the hot fluid gave rise to a peculiar sensation of pain in the immersed part: and so similar was the pain produced in each case, that from the sensation alone it was impossible to ascertain whether the fluid used in the experiment was hot or cold. Weber found also that when similar experiments were performed on the lips, the fingers, and other parts, their sense of touch was impaired in the same manner with regard to the perception of heat and cold: for, when two or more fingers were held immersed for a minute or so in water heated to 125° Fahr., or cooled to 32° Fahr., they were found to have lost, for a time, the power of discriminating between a hot and a cold fluid, or solid, body. As in the case of the tongue, so also here, a sense of pain was produced in the fingers during the immersion: this pain, which was the same whether the fluid was hot or cold, is probably to be referred to the trunk, not to the extremities, of the nerve of the immersed part.

He found also that it was not necessary, in order to the diminution or suspension of the sensitive powers of a nerve, that its extremities should

* Book the Fifth, p. 1059 of Müller's Physiology. † Müller's Archiv. 1847, p. 342.

undergo the exposure to heat or cold; for a similar effect was produced when the trunk of the nerve was acted on. The ulnar nerve is the one best suited to illustrate this fact, its trunk lying immediately beneath the surface at the elbow. After immersing the elbow in a mixture of ice and water for about sixteen seconds, Weber observed that a peculiar painful sensation was perceived along the under side of the fore-arm, the wrist, the little finger, and the inner side of the ring finger. The pain had no resemblance to that of cold. On continuing the immersion the pain increased considerably, and eventually became almost intolerable; then it gradually diminished, and the little and the ring fingers became numb, as if "asleep," had no longer the power of distinguishing between heat and cold, and could only imperfectly perceive the contact and pressure of bodies. The sense of smell also would appear, from Weber's experiments, to be for the time suspended, after the cavity of the nose has been filled with either hot or cold water. But the influence of heat and cold is, in this case, less certain, because the action of water alone, independent of its temperature, on the mucous membrane of the nostrils, will for a time suspend the sense of smell.

OF THE SENSE OF VISION.*

Tunics of the eye. The Tapetum.†—As will be mentioned again when noticing the structure of the retina, M. Brücke is of opinion that the staff-shaped bodies composing the so-called membrana Jacobi, probably serve the purpose of returning to the sensitive portion of the retina those rays of light which have traversed the retina, and which are not absorbed by the pigment of the choroid. M. Brücke‡ believes that this is peculiarly the case in those animals provided with a tapetum; and he considers that the function of the tapetum is to reflect the light on the staff-shaped bodies situated over that part of the retina most used in vision, and so to enable these animals to see, at times when animals unprovided with a tapetum would be in darkness. He observes that all the colours emitted in the dark from the eyes of animals possessed of a tapetum proceed from this structure alone, except the red, which is produced entirely by the blood in the large vessels of the retina and choroid. Hitherto the tapetum has been described as consisting, in all cases, of numerous undulating smooth and transparent fibres, so arranged as to form a fine membrane. But Brücke finds that although this, which he calls the *fibrous* tapetum, exists in most ruminants, Solidungula, and the whale tribe, yet in Carnivora this fibrous structure is replaced by another, composed entirely of smooth, nucleated, somewhat hexagonal-shaped cells; and this he calls a *cellular* tapetum. These cells vary from ·0008 to ·0028 of an inch in diameter; by transmitted light

* Book the Fifth, section i. p. 1088, Müller's Physiology. † Page 1119.
‡ Müller's Archiv. 1845, p. 388.

they are yellowish, and their nuclei pellucid; but by reflected light they have a beautiful blue colour, and the nuclei appear as small dark points.

Mr. Cumming* has found that the human eye, when observed under favourable circumstances, appears almost as luminous as the eye of the cat, dog, and other animals provided with a tapetum, to which this luminous appearance has been hitherto supposed to be limited. For the purpose of observing this in the human subject, the person whose eye is to be examined should be placed in a dark room, four or five feet from the half-closed door, with his face towards a light held at an equal distance outside the door. By such a contrivance the reflection may usually be perceived by an observer standing between the screen and the light, and occupying a position as near as possible to the direct line between the source of the light and the eye examined. It varies in appearance from a red livid glare to a bright golden red or burnished brass tint. In some individuals the phenomenon is much more manifest than in others; and in all, the brilliancy of the reflection is proportionate to the intensity of the light used in the experiment. Mr. Cumming is of opinion that the reflection takes place not from the retina, but from the choroid and its pigment. But Mr. Bowman † is disposed to consider it as proceeding from the hyaloid membrane and retina, as well as from the choroid.

The same luminous appearance of the human eye under favourable circumstances has been since noticed also by M. Brücke.‡ He observes that this phenomenon is less manifest in old than in young or adult persons,—a circumstance which he attributes to the greater quantity of choroidal pigment in the eyes of old than of young persons, to the less perfect transparency of the optic media of the eye, and to the more contracted state of the pupil commonly observed in old people. With respect to the source of this red glare, M. Brücke is of opinion that, in man, as in animals, it proceeds entirely from the blood in the vessels of the choroid and retina.

Iris.—The result of experiments recently performed by Signor Guarini,§ taken in conjunction with those obtained by Valentin, and Dr. J. Reid,‖ appear to leave no doubt that the movements of the iris are regulated by nervous influence derived from two different sources; the act of contraction whereby the aperture of the pupil is narrowed, being excited by the third pair of cerebral nerves, that of dilatation whereby the size of the pupil is enlarged, being dependent on branches from the cervical spinal nerves, which pass through the superior cervical ganglion of the sympathetic. Irritation of the third nerve, for example, causes contraction of the pupil,

* Medico-Chirurg. Transactions, 1846.

† Physiol. Anatomy of Man, by Dr. Todd and Mr. Bowman. Part iii. p. 51.

‡ Müller's Archiv. 1847, p. 225.

§ Annali Univ. di Med. 1844, and Gazette Médicale, 26 Avril, 1845.

‖ Müller's Physiol. Second Edition. vol. i. p. 827.

and division of this nerve is followed by dilatation. Irritation of the superior cervical ganglion, on the other hand, induces dilatation, while its destruction or removal is succeeded by contraction of the pupil. Moreover, after removal of this ganglion on one side, the application of belladonna, or administration of strychnine, is no longer followed by any marked dilatation of the pupil of the corresponding eye, but that of the opposite eye becomes extremely dilated. Besides thus proving the double source of nervous influence supplied to the iris, these experiments appear also to establish the truth of the opinion that dilatation of the pupil is as much the result of an active state of the iris as is its contraction, and that the one act is most probably produced by the radiating fibres of this structure, the other by the circular fibres situated around its inner margin.

The real nature of the fibres of which the iris is principally composed still remains obscure, although little doubt can exist that muscular tissue constitutes some portion of this membrane. Indeed, independent of the proof afforded by the rapidity of the iridal movements, and of their ready excitation on stimulating the nerves by which the iris is supplied, M. Brücke * states that the existence of a large quantity of fibres precisely analogous to those of which the muscular walls of the intestines are composed may be observed in the iris of the human eye, mixed up with the bundles of connective tissue which is frequently described as constituting the sole fibrous texture of this membrane. The existence of these muscular fibres in the iris of many animals, such as ruminants, appears to be doubtful. It is well known that in the iris of birds distinct muscular fibres possessed of transverse striæ are found in abundance; and that in accordance with this anatomical fact a voluntary power is possessed over the movements of this membrane.

The contraction of the pupil which ensues on irritation of the third nerve after death is never so complete as that observed during life, whereas the dilatation resulting from irritation of the superior cervical ganglion is as complete as during life. These facts are considered by M. Guarini to prove that some share in the contraction of the pupil during life should be attributed to venous congestion, resulting from compression of the blood-vessels interlaced among its fibres by the circular portion of the iris during its contraction. This is, probably, the utmost that can be effected by vascular turgescence towards the production of the iridal movements, although by many physiologists the contraction of the pupil has been regarded as almost entirely due to such turgescence, and its dilatation to an empty state of the vessels.

Irritation of the third pair of nerves does not appear in all cases to be followed by contraction of the pupil. Volkmann † found, for example, that although in dogs, after cutting off the head, and removing the brain,

* Müller's Archiv. 1846, p. 377. † Müller's Archiv. 1845, p. 414.

irritation of this nerve produced contraction of the pupillary aperture, yet in cats and rabbits such irritation, under similar circumstances, was succeeded by considerable enlargement of it. But before any weight can be attached to this statement, which is so entirely opposed to the experience of Valentin, Guarini, and others, it must be verified by the results of further observations.

Transparent Media of the Eye. Vitreous humour.—It has been pointed out by Pappenheim,* Ernst Brücke,† and more especially by Hannover,‡ that the vitreous body of the eye of many animals, as the horse, sheep, dog, and cat, is composed of concentric laminæ of structureless membrane, each of which forms a completely closed sac: the various sacs being enclosed one within the other. But the vitreous body of the human eye is shewn by Hannover to be composed of numerous sectors, the arcs of which are directed to the surface, while the angles converge towards the centre. Each sector consists of a fine textureless membrane derived from the hyaloid membrane, and enclosing the fluid of the vitreous body. The angles of the sectors do not quite reach the axis of the eye, but terminate in a homogeneous structureless substance situated immediately around the axis.

Structure of the retina.—Considerable addition has been made to our knowledge of the minute structure of the retina since the publication of the account given of it by Treviranus, and adopted by Professor Müller.§ It is essential to notice somewhat at length, the most recent information on this subject, inasmuch as it shews to be erroneous the ingenious explanation of the functions of the retina, founded on the supposed termination of its nerve-fibres in distinct papillæ.

These so-called papillæ, which are in reality the cylindrical or staff-shaped bodies composing the membrana Jacobi, are quite distinct from the nervous or sensitive portion of the retina; and, in the opinion of Henle || and Brücke,¶ belong more to the choroid coat, or at least to its pigmentary layer, than to the retina. A full description of these cylindrical bodies, and of the singular changes which ensue in them shortly after death, has been furnished especially by Hannover ** and Henle.†† It will be sufficient here to state that these bodies are transparent, highly refractive of light, and are arranged perpendicularly to the surface of the retina, and that their outer extremities are imbedded, to a greater or less depth, in the pigment of the choroid coat. The only plausible suggestion which has been offered concerning the use of these bodies, is one by Brücke,‡‡ who thinks it not unlikely that they may serve

* Specielle Gewebelehre des Auges, 1842, p. 182.
† Müller's Archiv. 1843, p. 345, and 1845, p. 130.
‡ Müller's Archiv. 1845, p. 471. § Physiology, p. 1122.
|| Allgemeine Anatomie, 1842, p. 662. ¶ Müller's Archiv. 1844, p. 444.
** Müller's Archiv. 1840, p. 340. †† Op. cit. pp. 656 and 783. ‡‡ Loc. cit. p. 444.

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to conduct back to the sensitive portion of the retina, those rays of light which, having traversed that membrane, are not entirely absorbed by the black pigment of the choroid; and he supposes that the individual rays returning through these highly refracting bodies may be directed to the same portion of the retina through which they had previously passed, and that their dispersion by mere reflection, which would tend to interfere with the distinctness of vision, is thus prevented. This view is rejected by Volkmann * as improbable.

Within the above described layer of staff-shaped bodies, is placed the expansion of the optic nerve in the form of a fine fibrous membrane, the individual fibres of which radiate from the point of entrance of the optic nerve, and pursue a tolerably straight course towards the anterior margin of the retina. At first the fibres run in distinct bundles, but these, by subdivision and a plexiform interchange of the individual filaments, speedily disappear, and for the remainder of their course the fibres are disposed in the form of a fine fibrous membrane, in which it is difficult to distinguish the several filaments. According to Dr. Todd and Mr. Bowman,† this expansion of the optic nerve appears to be composed of the gray or central portion alone of the individual fibres: the external white substance ceasing at the point where the optic nerve perforates the sclerotica. In the rabbit, indeed, the white substance is continued for a short distance within the globe, but even here the fibres speedily lose their white lustre, and assume for the remainder of their course the grey appearance observed in the fibrous layer of the retina elsewhere.

In defiance of the numerous attempts to determine the mode of termination of the nerve-fibres in the retina, the subject still remains in obscurity. It was supposed that Treviranus had discovered the true arrangement and ultimate disposal of the fibres, each of which was considered to terminate in a rod-shaped papilla on the internal surface of the retina: but it appears to have been clearly proved of late that this view is quite erroneous. The nature of the papillæ, as already observed, is quite different from that described by Treviranus, who, as well as others by whom his view was at once adopted, appears to have overlooked the peculiar structure of the fibrous expansion of the optic nerve. Several later observers, including Valentin, Bidder, and Pappenheim,‡ are of opinion that the fibres terminate in loops at the anterior margin of the retina: Krause § says he has observed these loops at every part of the retina, both in front and behind: whilst Hannover || states that they end in free extremities, but never in loops. Nothing, therefore, can at present be stated positively on this point, except that at the posterior part of the

* Wagner's Handwörterbuch, Art. Sehen, p. 272.

† Physiological Anatomy of Man. Part iii. p. 28.

‡ Canstatt's Jahresbericht, 1843, p. 108. § Canstatt's Jahresbericht, 1842, p. 169.

|| Müller's Archiv. 1840.

retina, where the sense of sight is especially developed, no nerve-terminations, looped or otherwise, have yet been found, (except by Krause,) and that, therefore, the opinion that each sensitive point of the retina corresponds to the extremity of a separate nerve-fibre is not founded in fact.

The observations of all who have recently examined the minute structure of the retina, concur in describing the existence of numerous cells and globules surrounding the fibrous expansion of this membrane, and situated chiefly along its internal surface and within the meshes formed by the interlacing of the individual nerve-fibres. These cellular bodies appear to be of different kinds, although, as Henle observes, it is probable that the several varieties met with, are only the same cells in different stages of development. The larger and more perfectly developed cells immediately surround the fibrous layer. By Valentin,* who first accurately described them, they were considered as identical with the ganglion-corpuscles of nervous substance. According to his account, which has since been generally confirmed, these cells when viewed separately are seen to consist of an external transparent membrane, granular contents, and a clear vesicular nucleus, containing a single particle in its centre. These cells lie closely packed together, and by this compression frequently lose their original round form. Valentin states that they are situated only on the internal surface of the fibrous expansion of the optic nerve, and within the meshes of this layer: Henle† makes a similar remark. But Hannover,‡ Krause,§ Pappenheim,|| and others have observed them on the external as well as the internal surface of this layer, which appears, therefore, to be imbedded in cells. The observations of Dr. Todd and Mr. Bowman¶ also, would seem to shew that the cells may occur on both sides. Pappenheim is of opinion that the fibrous expansion consists of two distinct laminæ: and Huschke, adopting this view, as well as the opinion that the cells are situated on both surfaces of the fibrous expansion, thinks that the external stratum of the cells corresponds to one lamina of the fibrous layer, the internal stratum to the other. Henle** discusses at some length, the question as to whether these vesicles should be regarded as analogous to ganglion-corpuscles, and is inclined to doubt the analogy. For, as he observes, beyond their general cellular character, they bear no other resemblance to ganglion-corpuscles; and he is of opinion that they probably constitute a kind of transparent epithelium, which serves to invest the delicate nerves composing the fibrous layer. Very shortly after death these cells break up, and the place which they occupied becomes a confused granular mass, in which are scattered, often in a linear direction,

* Repertorium, 1837, p. 25.
† Allg. Anat. p. 663.
‡ Müller's Archiv. 1840, p. 340.
§ Valentin's Repertorium, 1842, p. 169.
|| Huschke, Eingeweiden und Sinnes-org. des Menschl. Körpers, p. 719.
¶ Op. cit. p. 29.
** Op. cit. p. 665.

numerous oil-like globules, which are probably the nuclei of the disintegrated cells.

Between the above-described cells immediately surrounding the fibrous portion of the retina, and the internal surface of this membrane, other globular particles are found, smaller than the last.* They somewhat resemble blood-corpuscles, in form and size, and lie thickly together, but without adhering either to each other, or to the larger corpuscles. As was before observed, they are considered by Henle to be an early stage of development of the large cells, probably the nuclei; many, indeed, appear to be already surrounded with a delicate cell-wall, within which is a faintly-granular material. These cells occasionally present a very close resemblance to epithelium.†

Formation of images on the retina.—It has been found by Volkmann‡ that in order to perceive the image of a bright object depicted on the retina of a human eye, it is not necessary to make an opening into the sclerotic and choroid coats, as formerly directed,§ for it can be perceived through these tunics almost as distinctly as through the transparent tissues of the eye of the white rabbit or other albino animal. Moreover, he has found that this image may be observed in the eye even of a living person. For this purpose an individual should be selected in whom the eyes are large and prominent, and whose sclerotica possesses an unusual degree of transparency, as denoted by the bluish tint which it presents through the conjunctiva. When such an eye is directed as far outwards as possible, and a luminous object is then placed at the outside of it, at an angle of from 80° to 85°, the image of this object may be detected at the inner angle of the eye, appearing through the transparent sclerotica. Sometimes this image is so distinct that the inverted position in which the object is depicted on the retina may be clearly discerned.

Adaptation of the eye to vision at different distances.||

The power possessed by the eye of so adapting itself as to obtain a distinct view of objects placed at various distances from it, and thus of providing against the errors in vision which would otherwise result from the varying focal distances at which the perfect image of the objects would be formed on the retina, still continues to occupy the attention of physiologists; and although many ingenious attempts, both formerly and of late, have been made to account for this highly important property of the eye, no completely satisfactory explanation of it has been hitherto afforded.

* Valentin, Henle, &c. Op. cit.

† Klenke, in Canstatt's Jahresbericht for 1842, Physiologie, s. 315.

‡ Wagner's Handwörterbuch, Art. Sehen, p. 286.

§ Müller's Physiology, p. 1131.

|| Müller's Physiology, p. 1136.

Professor Müller has well discussed the whole of this subject,* and the additional observations which have been made since the period at which his account was published, consist less of new hypotheses than of arguments and fresh facts tending either to support or controvert one or other of the several explanations considered at length by him. In further refutation, for example, of the doctrine according to which this power of adaptation of the eye is attributed to an elongation of the entire globe, effected by compression of it through the action either of the four straight, or of the two oblique muscles of the eye, Hueck† states, that owing to the firmness and resistance of the sclerotica in the perfectly fresh eye, he was unable, even by considerable circular pressure, to produce any appreciable elongation in the globe of fresh eyes from a bird and from a cat; nor in consequence of such pressure did any remarkable alteration in the distinctness of an image formed on the retina ensue. He endeavoured also to ascertain the effects of such pressure on the eye of the living human subject, and for this purpose hollowed out a piece of cork, and adapted it to the globe of the eye in such a manner that he could thereby compress it against the inner wall of the orbit: and the result of such compression was the production of but a slight change in the distance of distinct vision.

The increased convexity of the cornea, which was said to be one of the important changes effected by compression of the eye, and on the occurrence of which its power of adaptation to the perception of near objects was supposed to depend, could not be detected by Hueck. He attentively watched the cornea while the sight was changed from an object thirty feet distant from the eye to one only seven inches distant, but beyond the movements resulting from respiration and from the pressure of the orbicularis muscle, he could not perceive any change in the cornea; no protrusion, and no sinking. This agrees with the observations of Dr. Young, who also was unable to perceive any such change as was said by Sir E. Home and others to take place.‡

Another mode in which the action of the recti muscles was supposed to aid the eye in adapting itself to the distinct vision of objects at different distances was by retracting the globe and compressing it against the posterior part of the orbit, whereby the axis of the eye would, it was sup-

* Physiology, pp. 1136–50.

† Ueber die Bewegung der Krystallinse, 1839, noticed by M. Tourtual in his Report on the Progress of the Physiology of Vision. Müller's Archiv. 1842, p. iii.

‡ Müller's Physiology, p. 1143. Mr. Smee (Vision in Health and Disease, page 16), acting upon the suggestion made by Professor Müller, has watched the images formed by reflection on the cornea, and states that when the eye looks at distant objects these images become smaller than when it is directed to near objects; if this change in size really ensues (though it is difficult to make quite sure about it) it would certainly seem to indicate that the convexity of the cornea undergoes some alteration at such times.

posed, be shortened, and the focal point of the rays from distant objects thus be made to impinge on the retina instead of falling short of it, as would be the case if some such adapting power did not exist. According to this view of the action of the muscles, therefore, their effect would be to render distinct the perception of distant objects only: but Hueck gives further proof that, as was observed by Professor Müller,* it is in looking at any near objects that we make an active change in the condition of the eye; the vision of distant objects being attended by a comparatively passive state of the organ. The existence, however, of any such alteration in the form of the eye by the action of the recti muscles is quite improbable, for, owing to the presence of a yielding mass of fatty tissue at the posterior part of the orbit, a very considerable, and, therefore, quite manifest, retraction of the globe must take place before the shortening of the axis of the eye supposed by this hypothesis could be effected. No such retraction, however, is observed to take place during any part of the act of vision. Indeed, as observed by Volkmann,† we do not seem to possess sufficient power over the recti muscles to produce the combined action of all the four at one time; and except by such combined action, either of all four, or at least of two opposite ones, retraction of the eye-ball could not be effected. There does not exist any obstacle to the retraction of the eye within the orbit, could the simultaneous action of the recti muscles be induced at will; this was shewn by Volkmann, who galvanised the third pair of nerves in animals recently slain, and observed well-marked retraction of the eye to ensue in consequence. Another circumstance mentioned by Volkmann,‡ to shew how little, if any, share is taken by the recti muscles in adapting the eye to vision at different distances, is that injury of the third pair of nerves, whereby paralysis of three of the recti muscles is produced, is not followed by any material disturbance of the power of adaptation; while, on the other hand, certain pathological conditions sometimes occur, in which, without any alteration in the functions of the muscles of the globe, the eye suffers a temporary impairment, or even permanent loss of this power.

In addition to the many proofs already afforded that the action of the *iris* is not the force concerned in adapting the eye to various distances of vision, and that alterations in the width of the pupil may take place without any corresponding change in the distinctness of objects under view, Hueck states that without altering the direction of the axes of his eyes, or the quantity of light admitted, but merely by fixing his attention on a side object, he was able to widen his pupils as much as one half more than their former diameter, without there ensuing any indistinctness of the object towards which the eyes were directed. He observes also that the inefficiency of the iris, in this respect, is demonstrated by the fact that

* Physiology, p. 1144. † Art. Sehen, in Wagner's Handwörterbuch, p. 301.
‡ Loc. Cit. p. 302.

individuals in whom the iris is wholly wanting have usually perfect vision for near as well as distant objects.

Volkmann and Hueck both agree in considering that in its quiescent state the eye is adapted to the vision of objects situated at the furthest point of distinct sight, and not, as has been generally supposed, of those situated about midway between this and the point of distinct vision nearest to the eye. In this case, therefore, in order to accommodate itself to the vision of an object placed at any distance within the furthest point of sight, the eye will require but one act, that, namely, of increasing its focal distance in proportion to the nearness of the object under view: no act will be requisite to adapt it to the perception of distant objects, for, in reverting to its state of rest, it at once resumes its capacity for distant vision, and retains it so long as its quiescent state continues. In proof of this opinion Volkmann observes, that in the state of rest the axes of the eyes are directed towards a point even considerably beyond the most distant point of distinct vision, and that, since changes in the position of the axes usually correspond with changes in the adaptation of the eyes, it is improbable that the meeting of the axes beyond the most distant point of vision should coincide with an adaptation of the eyes for an object on this side the point. According to Hueck this view will also explain the distinct formation of the image of distant objects on the retina after death; as also the far-sightedness induced by the action of hyoscyamus and of belladonna.

The tendency of most of the late observations on the subject of the accommodating power of the eye is in favour of the view proposed by Kepler, and countenanced by Professor Müller,* that this power is mainly due to some alteration either in position or form, or in both, undergone by the crystalline lens. The arguments stated by Hueck in favour of this view are, first, that if the eye is watched attentively from the side, the iris will be observed to be bent forwards in the middle and approximated closer to the cornea when a near object is viewed, and to become flattened again when the sight is fixed upon a distant object. And, secondly, that when the fresh eye of a dog is removed and placed before a window, so that a distinct image of the window-frame through an opening in the sclerotica, and an indistinct one of a smaller object, such as a key, held nearer to the eye, are perceived, the latter may be rendered distinct, and the former indistinct by drawing the lens forward with a needle inserted through the margin of the cornea. With respect, however, to the mode in which this supposed approximation of the lens towards the cornea during the vision of near objects is effected, different explanations still continue to be offered. Burow † adopts that view, according to which the forward movement of the lens is attributed to vas-

* Physiology, p. 1150. † Tourtual's Report (page xi), in Müller's Archiv. 1842.

cular turgescence of the ciliary processes; and in this Tourtual agrees with him. Mr. White Cooper * and Mr. Alfred Smee,† who have lately written on this subject, also advocate the same view. In Mr. Smee's opinion turgescence of the ciliary processes will produce pressure outwards against the cornea, and inwards towards the vitreous body, and the result of this will be that the lens is carried directly forwards; its subsidence to its former position will ensue passively on the cessation of the turgescence. But the most probable explanation, and one which has received the most support, is that the forward movement of the lens is effected by a contractile, probably muscular, tissue, situated in the parts surrounding the margin of the lens. According to many of the older observers, such a contractile tissue was supposed to exist in the lens itself; and this opinion was formerly entertained by Volkmann, who of late, however, has seen reason to abandon it. Hueck, who has especially occupied himself with the consideration of this subject, states that the contractile tissue by which the lens is acted upon is situated along the anterior and inner portion of the ciliary body, and consists of transversely arranged, firm, probably muscular fibres, connected together in a kind of network. Brücke's ‡ account corresponds very closely with this, though he considers the whole ciliary body to be composed of muscular fibres, which pass backwards to be inserted into the choroid coat. In birds, and many amphibia, he describes these fibres as being of the striped variety; but in man and mammalia they are unstriped. Huschke is of opinion that on the contraction of these fibres, which ensues during the vision of near objects, the fluid contents of the canal of Petit are compressed against the margin of the lens, whereby the lens itself is lessened in diameter, and becomes more curved forwards on its anterior surface. Brücke, on the other hand, considers that the action of these fibres will be to draw the choroid, and with it the retina closer around the vitreous body so as to compress it [and thus probably push the lens forwards, so as to assist in the vision of near objects]. On relaxation of these fibres the choroid regains its former position by the recoil of a layer of elastic fibres, which, according to Brücke, are situated between the ciliary body and the choroid. Dr. Clay Wallace,§ who was among the first to describe these muscular fibres of the ciliary body, considers that they act in adapting the eye to near vision by compressing the ciliary veins, and so producing the turgescence of the ciliary processes, which he, as well as the other observers already mentioned, recognizes as the cause of the accommodating power of the eye. According to Wagner,|| the ciliary processes as well as the ciliary body, contain contractile fibres, which have all the characters of those of organic muscle: by the action of these fibres, Wag-

* On Near and Distant Vision, 1847, p. 195.

† Vision in Health and Disease, &c. 1847.

‡ Müller's Archiv. 1846, p. 370.

§ London Medical Gazette, 1842. Dec. 16 and 23.

|| Lehrbuch der spezielle Physiologie, 1843. Second edition, p. 405.

ner considers that the lens may be drawn forwards as well as perhaps somewhat compressed laterally. Wagner's account of these fibres of the ciliary body and processes is also corroborated by the researches of Mr. Todd and Mr. Bowman,* who describe the fibres as radiating backwards from the junction of the sclerotic and cornea, and spreading over the outer surface of the ciliary body, the more superficial ones being inserted into the posterior part of this body, while the deeper ones seem to dip behind the iris to the more prominent parts of the ciliary processes which approach the lens. These fibres, although they belong to the unstriped variety of muscle yet seem to be analogous to those of the ciliary muscle in birds, which occupy the same position, but are of the striped kind. The contraction of these fibres will, according to Dr. Todd and Mr. Bowman, have the effect of advancing the ciliary processes, and with them the lens to which the processes are attached with considerable firmness, towards the cornea. One difficulty, however, which must ever present itself against the view that the contraction of these various fibres situated about and within the ciliary body—belonging, as they are said to do, to the class of involuntary muscles—constitutes the exclusive, or even the principal, condition by which the eye is enabled to accommodate itself to the distinct vision of objects at various degrees of closeness, is the circumstance that this accommodating power can by many persons be effected by a voluntary effort, quite independent of any alteration in the direction of the axes of the eyes. It cannot but be concluded from this circumstance either that there exist some other conditions than the contraction of the above described muscular fibres, by which the eye can adapt itself to distances, or else, which is very improbable, that a voluntary and tolerably rapid movement can be effected by the action of involuntary muscular fibres. The same difficulty occurs also in referring the explanation of the adapting power of the eye to vascular turgescence of the ciliary processes.

An entirely different explanation of the power of adaptation in the eye has been offered by M. Sturm.† This explanation is founded chiefly upon the result of Chossat's ‡ measurements of the eye of an ox, which shew that none of the refracting media of the eye have a spherical form, but that the anterior surface of the cornea and the two surfaces of the lens represent segments of different ellipsoids. From such a conformation of the refracting bodies it will follow that the several rays of a cone of light proceeding from an object placed before the eye will not be concentrated to a single focal point at a definite distance behind the lens, as is commonly supposed, but will intersect each other at different distances, within certain limits. And in any plane within these limits, although the rays are spread over a minute surface, instead of being collected to a point, yet

* Op. cit. Part iii. p. 27.

† Comptes Rendus, tom. xx. pp. 554 and 761.

‡ An. de Chimie et de Physique, tom. x. 1819.

the majority of them are situated at the centre, and will be capable of representing an image of the object regarded. Hence it results in Sturm's opinion that whether the object be approximated closer to or removed further from the eye, without any change in the eye itself, perfect vision of it will be obtained, the retina being still within the limits of the intersection of the rays. If, however, the position of the object before the eye be so much altered that none of its rays can cross each other at the retina the image of it will be indistinct.

Professor J. D. Forbes * has lately expressed an opinion that the adjusting power of the eye is due to the variable density of the crystalline lens. It is usually considered that the great difference in density between the central and peripheral portions of the lens is intended for the purpose of correcting the effect of spherical aberration of the rays of light, but Professor Forbes remarks that there is no need for the existence of such correction; for, as already mentioned, it has been shewn by M. Chossat's measurements,† that the lens does not represent the segment of a sphere, but of an ellipsoid, in which the surfaces have a curve of *no aberration*, and will consequently require no variation in density of the refracting medium. This Professor Forbes regards as a proof that the variable density of the lens is intended for some other purpose than to correct aberration: and this purpose he conceives to be the focal adjustment of the eye. In order to render the lens available for the production of this object, he believes that in regarding a near object the four recti muscles of the eye are simultaneously and voluntarily set in action, whereby the eye is drawn back into the socket, and that the pressure thus resulting upon the humours of the eye is propagated to the lens, which, owing to the inconsiderable density and elasticity of its peripheral parts, is altered from its flattened ellipsoidal form to a somewhat more spheroidal mass, and one possessed of greater density than before. In this manner its converging powers will be increased, and distinct vision of a new object thus be effected. Against this ingenious view, however, must be repeated the several objections, which have been already stated at page 22; namely, the absence of any firm resisting medium at the posterior part of the socket, which is chiefly occupied by fat: no appearance, during the vision of near objects, of any retraction of the globe of the eye, which probably must ensue before the action of the recti muscles could exert such compression on the lens as to produce the effect supposed by Professor Forbes; and lastly, the objection urged by Volkmann against the probability of any share in the adjusting property of the eye being taken by the recti muscles, namely, that we do not appear to possess the power of voluntarily exciting all the recti muscles to simultaneous action.

From the consideration of these several opinions offered in explanation

* Transact. of the Royal Society of Edinburgh, 1845, part i. † Ann. de Chimie, l. c.

of the remarkable property possessed by the eye of accommodating its visual powers to the distinct perception of objects placed at such various distances from it, the conclusion naturally forces itself upon the mind, either that we still remain unacquainted with the real cause of this singular property, or, which is more likely true, that it is the result of two or more of the above-mentioned conditions acting together. For by thus attributing to several of these conditions a certain relative share in the production of this result, it is easy to perceive how by their united agency, they may effect that alteration in the interior of the eye on which the focal adjusting power of this organ depends, but which, individually, it is improbable they could induce.

The range of distance through which the human eye is capable of adapting itself to distinct vision, has occupied the attention of Hueck and Burow.* Both observers have found that this distance varies in different individuals, whose sight in other respects may be quite perfect; and Burow observes that, as a rule, there is a close correspondence between the position of the most distant and that of the nearest point of vision, so that the one being determined, the other may be inferred with tolerable accuracy. The distance between the two bears a close relation also to the refractive power of the eye, being less in proportion as the latter is greater, and *vice versâ*. According to Volkmann, the eyes of different individuals likewise vary in their comparative refracting power over the circumferential and central rays of light; in some persons the former rays are refracted more powerfully than the latter, while in others the reverse is the case. A series of experiments conducted by Gruber,† led him to the conclusion that even in the same individual, the two eyes have frequently dissimilar distances for distinct vision, so that an object which apparently is regarded by both eyes, is in reality distinctly seen only by one, the focal distance of the other eye requiring to be altered, in order that it likewise may have a clear sight of the object.

In a case of singular congenital malformation of the iris in which the transverse diameter of the pupil was considerably greater than the longitudinal, the latter not exceeding in its middle or widest part, half a line, in a moderate light, and the entire pupil completely closing in a strong light, Tourtual‡ found, among other peculiarities of vision, that objects having a transverse direction could be perceived at a greater distance than those which were longitudinal. This, and other circumstances, led him to the conclusion that a transverse pupil will have the effect, like the opening between the eyelids, of increasing the distinctness with which distant objects are perceived.

* Beiträge zur Physiol. und Physik des mensch. Auges, 1842. Noticed by Tourtual, Loc. Cit. p. vii.

† Canstatt's Jahresbericht. 1847, p. 194.

‡ Müller's Archiv. 1846, p. 346.

*Action of the retina and of the sensorium in vision.**

Under this head may be mentioned some of the highly interesting particulars of a case in which a well-informed youth, blind from birth, had the sight of one eye restored by a successful operation performed by Dr. Franz.† The patient had congenital cataract of both eyes, with internal strabismus to such a degree, that nearly one half of each cornea was hidden by the inner canthus. The right eyeball had atrophied in early life, in consequence of inflammation ensuing after the operation of keratonyxis, and became completely amaurotic. The left retained sensibility to the impression of light, but had no power for the perception of objects. At the age of seventeen the operation for cataract was successfully performed on the left eye, and the sensitiveness of the retina was at once made evident by the blaze of light perceived when the eye was opened. On the third day after the operation, the eye was again opened, when the patient perceived an extensive field of light in which no object could be distinguished: everything appearing dull, confused, and in motion. During the next few days, at the times of the eye being open, nothing was seen except a number of " opaque watery spheres, which moved with the movements of the eye, but, when the eye was at rest, remained stationary, and then partially covered each other." The spheres gradually became more transparent, and the patient was enabled to perceive, through them, as it were, a slight difference in surrounding objects: but, owing to the pain produced by the light, the eye could not be kept open long enough to allow of a distinct visual impression of any object being perceived. The appearance of spheres had entirely vanished at the end of two weeks. When the intolerance of light had so far abated that the patient could, without pain, regard an object for a sufficient time to gain a clear idea of it, he was able to perceive and correctly describe vertical and horizontal lines, triangles, spirals, and other black figures drawn on paper and placed before him. His perception and discrimination of different colours placed on a black ground were equally correct. An answer to the well-known question put by Mr. Molyneux to Locke‡ was next experimentally sought. A solid cube and a sphere, each of four inches diameter, were placed before the patient at the distance of three feet, and on a level with the eye. " After attentively examining these bodies, he said he saw a *quadrangular* and a *circular* figure; and, after some consideration, he pronounced the one a *square*, and the other a *disc*. His eye being then closed, the cube was taken away, and a disc of equal size substituted, and placed next to the sphere. On again opening his eye, he observed no difference in these objects,

* Müller's Physiology, p. 1162. † Philosophical Transactions, 1841, pp. 59—68.
‡ Müller's Physiology, p. 1176.

but regarded them both as discs. The solid cube was now placed in a somewhat oblique position before the eye, and close beside it a figure cut out of pasteboard, representing a plain outline prospect of the cube when in this position. Both objects he took to be somewhat like flat quadrates. A pyramid placed before him, with one of its sides towards his eye, he saw as a plain triangle. This object was now turned a little, so as to present two of its sides to view, but rather more of one side than of the other: after considering and examining it for a long time, he said that this was a very extraordinary figure; it was neither a triangle, nor a quadrangle, nor a circle: he had no idea of it, and could not describe it: 'in fact,' he said, 'I must give it up.'" An example of the close association which exists between the sense of touch and that of sight in enabling the mind to form a correct idea of an object, is afforded in the statement of this patient, that, although, by the sense of sight he could detect a difference in the cube and sphere, and perceive that they were not drawings, yet he could not form from them the idea of a square and a disc, "until he perceived a sensation of what he saw in the points of his fingers, as if he really touched the objects." When he took the sphere, cube, and pyramid, into his hand, he was astonished that he had not recognized them as such by sight, being well acquainted with them by touch.

When the patient first acquired the faculty of sight, all objects appeared much nearer to him than they really were, and much larger than he had supposed them to be from the idea obtained by his sense of touch. He also saw everything perfectly flat: and, by the sense of sight alone, could obtain no correct idea of a solid or projecting body. When, by the division of the internal rectus muscle of both eyes, effected about two months after the operation for cataract, the strabismus was cured, all objects were, for a considerable time afterwards, seen much to the right of their real position. These various circumstances shew how large a share is taken by the operations of the mind in association with the impressions received on the retina, in forming a correct estimate of the form, size, distance, and position of an object presented to the sight, and how difficult it is in the case of the educated eye to say "what belongs to mere sensation, and what to the influence of the mind," *

Physiological colours produced by contrast.—Some interesting observations with respect to the formation of complementary colours, have been published by Dr. Tourtual.† On moving rapidly to and fro a pen-knife in front of the white glass shade of a burning lamp, Dr. Tourtual observed that it assumed a beautiful blue colour, the distinctness of which was in direct proportion to the rapidity of the movements. On the cessation of these movements the colour changed into black. The introduction of a

* Müller's Physiology, p. 1166. † Canstatt's Jahresbericht, 1845, p. 208.

second light prevented the occurrence of the phenomenon. The blue colour was considered by Dr. Tourtual to be complementary of the reddish-yellow colour of the lamp; and he was led by the circumstance to undertake some additional experiments on the subject. On placing a strip of black silk, about three lines broad, on a piece of orange-coloured cloth, and on directing the axes of both eyes towards it at a moderate distance, and in clear daylight, the distinction between the two colours was clearly seen. But on closing the left eye, and gradually approximating the object towards the right eye, whose direction and point of adaptation remained unaltered, a bright margin appeared around the black silk, and the silk itself assumed a dark blue colour. When, in a similar experiment, the black silk was placed on a purple ground it assumed a green colour, on a violet ground a yellow colour, and so on; the colours assumed being always complementary of that on which the silk was placed. A similar phenomenon was observed when, instead of the black silk, a strip of white paper of the same breadth was employed. The change of colour may be observed also, when, instead of altering the position of the object, the eye be directed to a point about an inch on one side of the black stripe; or when the one or both eyes are made to accommodate themselves to distant vision. The size of the pupil has no direct influence on this phenomenon; it appears, in the opinion of Tourtual, to arise from indistinctness of vision alone.

An interesting fact in relation to complementary colours, has also been noticed by M. Brücke.* He found that the transmitted portion of the rays of light falling on any given part of the fibrous tapetum of animals, possessed a colour exactly complementary of that reflected by the same part of the tapetum. The various colours reflected by the tapetum (not including the *red*, which is due to the blood in the vessels of the retina and choroid) are yellow, merging into orange, yellow itself, green, blue, and blue merging into violet; those transmitted are all complementary of these, viz., violet merging into blue, violet itself, red, orange, and orange merging into yellow.†

Relation of non-luminous rays to the eye.—Several very ingenious experiments have been performed by Ernst Brücke,‡ to determine whether the chemical and calorific rays of light are transmitted through the transparent media of the eye as well as the luminous ones. To ascertain this with regard to the chemical rays, those namely which are situated outside the violet, he took advantage of the property which these rays possess of changing the colour obtained from guaiacum wood first to a bright green, and then to a deep greenish-blue tint. Having coloured a small porcelain plate with tincture of guaiacum and dried it in the dark,

* Müller's Archiv. 1844, p. 449.

† For an account of the Simple and Complementary colours, see Müller's Physiology, p. 1103.

‡ Müller's Archiv. 1845, p. 262.

he allowed light to fall on it, after passing through the fresh lens of an ox's eye. The result was, that instead of being deeply coloured, as it would have been by ordinary diffused light, it scarcely underwent any change. The experiment was then performed with the cornea as the transparent medium, then with the vitreous humour, and lastly with all the three media together. And the general results which he obtained were, that the lens, instead of allowing the chemical rays to pass through it, absorbs them very largely; that the cornea and the vitreous humour absorb them also, though in a less degree; and that with the three media together, the absorption is almost complete. In a more recent set of experiments,* he obtained equally satisfactory results by employing photographic paper as the sensitive surface on which the rays of light were allowed to fall after traversing the transparent media of the eye. The results of these latter experiments proved, at least, that those rays situated to the outside of the violet are arrested, although the paper was deeply blackened by the violet ray itself.

To determine the same point in regard to the calorific rays, M. Brücke made use of a thermo-electric apparatus, and on allowing light to fall on this through the transparent media of the eye, he observed that its needle underwent no change; shewing, therefore, that very little, if any, of the calorific portion of a ray of light is transmitted through the eye.

Binocular vision.—A somewhat different explanation of the mode in which the reflection of two different views of a solid object in the stereoscope † produces in the mind the idea of a single object similar to the original, has been proposed by Tourtual,‡ who details the results of numerous experiments in support of it. But in this explanation there appears to be little really at variance with the one afforded by Professor Wheatstone, and in the results of the experiments nothing which can invalidate the main conclusion derived from Professor Wheatstone's philosophical researches, namely, that our conviction of the solidity of an object, or of its projection in relief, is due, in great measure, to the circumstance of corresponding portions of the two retinæ receiving the impression of a different view of the object—the one view as seen by the right eye, the other by the left—whereby an exact counter-part of the original is produced. Tourtual objects to this view, and considers that the fact of the solidity of a near object being distinctly realized by one eye alone, affords a conclusive proof that the visual perception of an object of three dimensions, is an operation of the mind, and is not necessarily dependent on the formation of two images of this object on the retinæ. Volkmann and Brücke also appear to agree with Tourtual in the opinion that the perception of a solid object in the

* Op. Cit. 1846, p. 379. † Müller's Physiology, p. 1205.

‡ Report in Müller's Archiv. 1842.

field of vision does not result from a coalescence of two perspective views of it depicted on the retinæ, but that the single idea thus excited, is the product entirely of a mental operation, by which a single form is created from the two images presented to the retinæ. The distinction is one obviously unimportant, and has probably arisen from these observers having under-estimated the amount of mental influence admitted by Professor Wheatstone to be concerned in the true visual perception of a solid body.*

OF THE SENSE OF HEARING.†

Movements of the small bones of the ear.—In an account of the movements undergone by the small bones of the ear, and their utility to the sense of hearing, Ed. Weber ‡ offers an explanation of the rounded appearance presented by the external surface of the membrane of the fenestra rotunda when the membrana tympani is pushed inwards after death, and of its concave appearance when the membrana tympani is drawn outwards. He observes that the articulation between the head of the malleus and the body of the incus is such that the former bone cannot be moved alone by the membrana tympani, but that both move together as one bone. He states that their axis of movement is the line drawn from the slender process of the malleus to the short process of the incus; on these two processes adherent to the wall of the tympanum the bones turn, as on a pivot. Thus it happens that when the membrana tympani is pushed inwards, the stapes is pressed within the fenestra ovalis by the long process of the incus; when, on the contrary, the membrana tympani is drawn outwards, the stapes is carried out from the fenestra ovalis. The stapes could not exercise these movements completely if the cavity of the labyrinth was bounded entirely by firm and unyielding walls, for the fluid within it is almost incompressible. But by the pressure of the fenestra rotunda this difficulty is avoided. The fluid which fills the vestibule communicates with that in the cochlea, particularly with that of the scali vestibuli, which again freely communicates with that of the scala tympani; so that when the membrane of the fenestra ovalis is pushed inwards towards the vestibule, the consequent pressure on the contained fluid will be communicated to the membrane of the fenestra rotunda, which will be pushed outwards. In this way the movements of the membrana tympani produce indirectly the flux and reflux of the fluid of the labyrinth from the fenestra ovalis to the fenestra rotunda, by percussion, and by the yielding of the lamina spiralis of the cochlea.

* See Müller's Physiology, pp. 1200 and 1206.

† Section ii. p. 1215, Müller's Physiology.

‡ Archiv. d'Anat. Physiol. Janvier, 1846, p. 16.

RECENT ADVANCES

IN THE

PHYSIOLOGY OF GENERATION.

OF THE UNIMPREGNATED OVUM.*

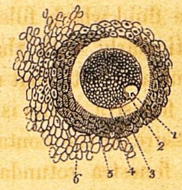
The observations of Bischoff and other inquirers relative to the structure and anatomical relations of the unimpregnated mammiferous ovum, which have been published since the commencement of 1842, have, for the most part, only confirmed the accuracy of results previously obtained. In a few instances, however, they have served to correct erroneous views or to settle questions which were before disputed.

It is well known that the ovum, when mature, lies at that part of the Graafian follicle which forms a prominence on the surface of the ovary, and is imbedded in a thickened portion (discus proligerus) of the layer of nucleated cells (membrana granulosa of Baer) which lines the follicle. The statement of Dr. Barry that the ovum is retained in this position by a peculiar apparatus, called by him the retinacula, has received no confirmation. Bischoff† expressly declares that he has never seen anything resembling such a structure.

Some recent observations on the intimate structure of the coats of the *Graafian follicle* will be detailed at page 53.

The *parts composing the ovum* are, 1. the external thick transparent tunic, known as the zona pellucida; 2. the yolk; and 3. the germinal vesicle with the germinal spot (see fig. 2). The investment of the ovum external to the zona pellucida, which Dr. Barry named tunica granulosa has no existence as a distinct and independent structure. It consists merely of an adhering layer of the cells belonging to the membrana granulosa in which, as has just been stated, the ovum is imbedded.

Fig. 2.‡



The doubt whether the *zona pellucida* be really a solid, transparent,

* Book vii. sect. ii. chap. iii. p. 1464 of Müller's Physiology.

† Entwickelungs-geschichte der Säugethiere und des Menschen. Leipzig, 1842, p. 10.

‡ Ovum of sow, after Barry. 1. Germinal spot; 2. Germinal vesicle; 3. Yolk; 4. Zona pellucida; 5. Tunica granulosa of Dr. Barry; 6. Adherent granules or cells.

structureless membrane, or a layer of albuminous fluid enclosed between two thin membranes, seems now to be resolved. Wagner, * Bischoff,† Henle, ‡ Barry,§ and Wharton Jones, || all adopt the former view respecting the nature of this part.

It is still, however, a disputed question whether internal to the zona pellucida there is not a second membrane enclosing the mass of yolk. Dr. Herman Meyer has stated ¶ that after he had completely dissolved the zona pellucida of an ovum, by the agency of a solution of potash, he ruptured the yolk, and allowed the yolk-granules to escape, and then saw a thin granulated membrane remaining, which had formed the proper investment of the yolk. Bischoff, however, has repeated this experiment, and affirms that in ova of the sow, cow, bitch, and rabbit, solution of potash does not dissolve the zona pellucida, but only produces contraction and condensation of it.** Meyer's observation seems, therefore, to have been an erroneous one; and as the membranes of which Dr. Barry has described †† the successive formation and disappearance on the interior of the zona pellucida, cannot be regarded as constituting an essential part of the ovum, all proof of the existence of any membrane internal to the zona pellucida, derived from actual observation, fails. Wagner ‡‡ infers that such membrane exists, from the fact that an interval can sometimes be seen between the zona pellucida and the yolk, and that the latter has then a very defined outline. But Bischoff,§§ as we shall presently see, gives a different explanation of this appearance, and denies positively that there is any other membrana vitelli than the so-called zona pellucida. Wharton Jones,|||| Coste, and Henle entertain the same opinion.

The *yolk* is described by Henle ¶¶ as being composed of granules and globules of different sizes, imbedded in a more or less fluid substance. The smaller granules, which are the more numerous, in their appearance as well as their constant motion, resemble pigment granules. The larger granules or globules, which have the aspect of fat globules, are in greatest number at the periphery of the yolk. The number of the granules is, according to Bischoff's observations, greatest in carnivorous animals. In the human ovum their quantity is comparatively small.

The substance that combines the globules and granules of the yolk is, in many animals, quite fluid. The yolk then completely fills the cavity of the zona pellucida, and escapes in a liquid form when that membrane is rup-

* Lehrbuch der Physiologie, 2te Ausgabe. Leipzig, 1843, p. 37.

† Entwickelungs-geschichte, p. 12; and more recently in his Entwickelungs-gesch. des Hunde-eies, 1845, p. 9.

‡ Allgemeine Anatomie, p. 965.

§ Researches on Embryology.

|| Lond. and Edinb. Phil. Mag. 1835, p. 209.

¶ Müller's Archiv. 1842, p. 18.

** Op. cit. p. 553.

†† The views of Dr. Barry are explained in the notes at pages 1499 and 1514 of Müller's Physiology.

‡‡ Op. cit. p. 37.

§§ Op. cit. p. 14.

|||| Med. Gazette, vol. xxi. and vol. xxiv.

¶¶ Allgemeine Anatomie, p. 966.

tured: but in ova of the human subject and some other animals the yolk is much more consistent, and sometimes escapes as a solid globular mass when the zona pellucida is torn. It is, according to Bischoff, solely owing to this firm consistence of the yolk that it, in many cases, preserves its form when a watery fluid passes by imbibition through the zona pellucida, and that an interval is then apparent between the yolk and that membrane.

Owing to the tough consistence of the yolk in the human ovum, Bischoff has not succeeded in isolating its *germinal vesicle;* but he has satisfied himself that it lies near the periphery of the yolk, though not imbedded in a discus proligerus, as it is in the bird's egg.*

The *germinal spot* which lies at that part of the periphery of the germinal vesicle which is nearest to the periphery of the yolk, presents in the mammiferous ovum no appearance of a vesicle or aggregation of cells, but merely that of a finely granulated substance, of a yellowish colour, strongly refracting the rays of light.†

The subjoined table gives the measurements of the mammiferous ovum and its different parts.

	Animal.	Measurements in parts of a Paris inch.	Observer.
Diameter of mature ovum.	Man	$\frac{1}{240}$ to $\frac{1}{120}$	Bischoff.
	Rabbit	$\frac{1}{156}$	Ditto.
	Bitch	$\frac{1}{147}$ to $\frac{1}{142}$	Ditto.
Thickness of zona pellucida	Man	$\frac{1}{2500}$	Ditto.
	Rabbit	$\frac{1}{2500}$ to $\frac{1}{1250}$	Ditto.
	Bitch	$\frac{1}{1666}$ to $\frac{1}{1250}$	Ditto.
Germinal vesicle. . . .	Rabbit, Bitch	$\frac{1}{166}$	Ditto.
Germinal spot.	Bitch	$\frac{1}{2500}$	Ditto.
	Mammalia generally	$\frac{1}{3600}$ to $\frac{1}{2400}$	Wagner.
Large yolk globules. . .	Ditto	$\frac{1}{6000}$ to $\frac{1}{4000}$	Henle.

Development of the ovum in the ovary.—The process by which the ovum is formed and brought to its state of maturity is scarcely noticed by Professor Müller. The enquiries of Dr. Barry are not mentioned by him, and those of Valentin only alluded to in a single line. It will be necessary, therefore, to premise here some account of their observations before detailing the results of the more recent researches of Bischoff.

The questions which it seems most important to decide by the aid of the facts revealed by these anatomists are the following:—

1. Is the Graafian follicle the immediate formative organ of the ovum?

2. In what order are the different parts of the ovum formed?

3. What changes do they undergo in the progress of the ovum towards maturity?

* Op. cit. p. 15. † Ibid. p. 15 and p. 556.

In the first stages of the development of its internal structure, the ovary, according to Valentin,* closely resembles the testis. A number of streaks are first seen running from the surface of the organ towards the solid axis. These streaks become tubes closed at either extremity, and having membranous walls lined with epithelial globules. In the cavity of these tubes, which are distinctly visible in the embryos of sheep or cows from three to five inches in length, the ovarian follicles are soon developed in the form of cellules, with transparent walls and granular contents, arranged in a linear manner. In proportion as the follicles increase in number and size, the walls of the tubes in which they are contained become thinned, and the central solid axis of the ovary relatively smaller. At length the tubes become so pressed together and displaced by the enlargement of the follicles within them, that the tubular structure is scarcely recognisable. Nevertheless, with some patience the tubes may be distinguished and even demonstrated separately in the young calf, sheep, cat, and rabbit, at the time of birth. While the Graafian follicles enlarge, their contents become more fluid. The fluid part collects in the middle of the follicle, while the granules which from the first have a linear arrangement form an investment, the membrana granulosa, on the inner surface of the follicle. The order in which the different parts of the ovum are developed, Valentin could not ascertain.

These observations of Valentin, though detailed as if they were made with great care, have not been confirmed by either Barry or Bischoff.†

Dr. Barry,‡ it is true, does not appear to have examined the state of the ovary in fœtal animals. It was in young animals, and in those which had just reached puberty that he studied the subject.

The results at which he arrived were that there is a continual disappearance of ova and formation of new ones from a very early age,—that myriads of ovisacs with their contents are formed which never reach maturity, and that the stroma of the ovary always contains innumerable groups of these immature ovisacs. The part first formed, however, according to Dr. Barry, is not the ovisac but the germinal vesicle. This becomes surrounded by a coating of oil-like globules and peculiar granules, and subsequently by a membrane which is the ovisac or Graafian follicle. The ovisac, as yet transparent and structureless, enlarges, and the granules within increase in number. Next a clear space forms around the germinal vesicle, which occupies the centre of the ovisac. In this space the oil-like globules accumulate, and minute opaque granules show themselves amongst them. Thus is formed the yolk, which next becomes separated from the granules in the general cavity of the ovisac by the development

* Müller's Archiv. 1838, p. 526, *et seq.*

† Bischoff expressly states that he has never seen the streaks and tubes described by Valentin, though he sought them in the embryoes of several mammiferous animals, of different ages.

‡ Philosoph. Transact., 1838.

of the membrana vitelli, and zona pellucida (now regarded as one membrane). The ovisac, or Graafian vesicle, subsequently acquires an external vascular tunic composed of dense cellular tissue.

M. Bischoff * agrees with Dr. Barry that the development of the Graafian follicles and ova continues uninterruptedly from birth to the end of the fruitful period of woman's life. In some animals, as the cow and sow, it commences in the embryo, even at an early period of uterine existence, but in the dog and rabbit, according to his observation, not till after birth.

M. Bischoff describes the process of formation of the Graafian follicles and ova to be as follows:—At first nothing can be distinguished in the substance of the ovary but primary cells and nuclei of cells. Then round groups of similar cells are seen scattered in large numbers through the stroma. The peripheral cells of each of these groups subsequently coalesce so as to form a homogeneous transparent vesicular membrane, while the portion of the mass within becomes fluid. Thus is formed the Graafian follicle. On the inner wall of this follicle or vesicle new cells are formed in the manner of an epithelial layer, while the cavity is found to contain a transparent fluid with nuclei of cells and granules, exactly resembling yolk granules, suspended in it. The next stage is marked by the appearance of a second smaller transparent vesicle within the Graafian vesicle. This second vesicle, which is the germinal vesicle, has a nucleus, the germinal spot. Granules, similar to yolk granules, soon accumulate around the germinal vesicle; but the further steps in the development of the ovum could not be traced. All its parts were completely formed when M. Bischoff next observed it.

From the preceding account of the observations of Valentin, Barry, and Bischoff, it will be seen that the first and the last of these enquirers agree as to the fact of the ovum being developed within the Graafian vesicle as *its immediate formative organ*, although they differ as to the process by which the Graafian vesicle itself is formed. Bischoff regards the statement of Dr. Barry that the germinal vesicle of the ovum exists before the Graafian follicle as altogether an error.

With regard to the second question proposed at page 35, namely, *in what order are the different parts of the ovum formed?* it appears a matter of certainty that the formation of the germinal vesicle precedes that of the yolk, and the yolk membrane. The observation of Dr. Barry as to this point is entirely confirmed by Bischoff. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals. But some recent observations of Kölliker † and Bagge ‡ on the development of the ova of intestinal worms show that in these animals the first step in the process is the

* Entwickelungs-geschichte, p. 365. † Müller's Archiv. 1843, p. 72.

‡ Diss. de Evolut. Strongyli auricular. et Ascaridis acuminat. Erlangæ, 1841.

production of round bodies resembling the germinal spots of ova, the germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

The more important *changes that take place in the ovum subsequent to the formation of its essential component parts* consist in alterations of the size and position of those parts with relation to each other, and of the ovum itself with relation to the Graafian follicle, and in the more complete elaboration of the yolk.

The earlier the stage of development the larger is the germinal vesicle in relation to the whole ovum, and the ovum in relation to the Graafian follicle. For, as the ovum becomes mature, although all these parts increase in size, the Graafian follicle enlarges most, and the germinal vesicle least. Changes take place also in the position of the parts. The ovum at first occupies the centre of the Graafian follicle, but subsequently is removed to its periphery. The germinal vesicle, too, which in young ova is in the centre of the yolk is in mature ova found at the periphery.*

The change of position of the ovum from the centre to the periphery of the Graafian follicle is probably connected with the formation of the membrana granulosa which lines the follicle. For, according to Valentin,† at a very early period the contents of the follicle between its wall and the ovum is almost wholly formed of granules, but in the process of growth a clear fluid collects in the centre of the follicle and the granules which from the first have a regular arrangement are pushed outwards, and form the membrana granulosa. Now as the mature ovum lies imbedded in a thickened portion of the membrana granulosa, it seems probable that when the elementary parts of this membrane are pushed outwards in the way just described, the ovum is carried with them from the centre to the periphery of the follicle. While the changes here described take place, the zona pellucida increases in thickness.

With reference to the yolk Valentin ‡ stated that it was richer in granules the younger the ovum. But Bischoff § affirms that the reverse of this is the fact. He says, that in almost all animals the number of the granules of the yolk is greater the more mature the ovum, and that the yolk consequently is more opaque in the mature, and more transparent in the immature ova. The matter in which the granules are contained is, according to Bischoff, fluid in the immature ova of all animals. In some it remains so; but in others, as the human ovum, it subsequently becomes a consistent gelatinous substance.

* See Bischoff, Barry, Henle, Wagner, Valentin, operibus citatis.

† Müller's Archiv. 1838, p. 533.

‡ Müller's Archiv. p. 534, 1838.

§ Entwick. d. Kaninchen-eies, p. 9; and Entwick. des Hunde-eies, 1845, p. 8.

OF THE SEMEN.*

THE few additions which it is necessary to make to the chapter on the subject of the semen, in the Physiology of Professor Müller, may be arranged under the following heads:—

1. Varieties of form presented by the spermatozoids or spermatic filaments.
2. Their structure.
3. Their motion.
4. The influence of reagents upon them.
5. Their modes of development.
6. The question of their independent vitality.
7. Their function.

1. It would serve no good purpose to repeat here the description given by Kölliker † and other recent observers ‡ of the forms of the spermatic filaments in the many species of invertebrate animals, in which they have recently been examined. The general result at which Kölliker arrived, with reference to the forms of the spermatic filaments was, that the varieties of form, though manifold, are comprised within tolerably narrow limits; that the forms are almost always very similar in the same *genus*, and mostly so even in the same *family* and *class;* while in the same *species*, never more than one form is met with.§ The apparent varieties of form observed in certain instances in the same species of animals, are, according to Kölliker's observations, only different stages in the development of one form of spermatic filament.

2. The notion that the spermatic filaments have an internal animal organization, is now abandoned by the best inquirers on the subject. Kölliker || declares that all the hair-shaped filaments, whether spiral or not, are formed of a homogeneous substance. The same is the case, also, he says, in by far the greater number of those that have a body distinct from the filamentous part. With regard to the spermatozoid of the Bear, Kölliker remarks that the circles imagined by Valentin ¶ to be mouth, convoluted intestinal canal, and anus, may have been merely the appearances

* Book vii. sect. ii. ch. iv. p. 1471, of Müller's Physiology.

† Beiträge zur Kenntniss der Geschlechts-verhältnisse und der Samen-flussigkeit wirbelloser Thiere, Berlin, 1841.

‡ Stein, Müller's Archiv. 1842, p. 238. Von Siebold, Müller's Archiv. 1843, p. 21. Rathke, Wiegmann's Archiv. 1842, i. p. 73. H. Meckel, Müller's Archiv. 1844, p. 473. Will, Horæ Tergestrinæ and Wiegmann's Archiv. 1844, Bd. i. p. 337. Paasch, De Gasterop. nonnull. hermaph. system. genitali et uropöetico. Diss. Berol. 1842. Müller, Ueber den Bau des Pentacorinus caput Medusæ, Berlin, 1843, p. 177.

§ Kölliker, Op. cit.

|| Op. cit. p. 64.

¶ See Müller's Physiology, p. 1473.

presented by the granules of which the spermatozoid was formed.* Mr. Gulliver † has recently had the opportunity of examining these spermatozoa, and declares that he could detect neither mouth, arms, nor internal vesicles. The dark spot seen in the body of the spermatic filaments of some mammalia, and compared by some writers to a sucker, is believed by Henle,‡ to be caused merely by a slight concavity similar to that on either side of the human blood-drill. Several observers § have noticed that in many of the spermatozoids of the human subject there is, at the junction of the body with the caudal filament, a gelatinous mass or membranous appendage. This appearance, as well as the little prominences on the body and knots on the caudal filament, which are sometimes seen, is probably due to their mode of development, and, at all events, is no evidence of independent animal organization.

3. The rate of the *motion* of the spermatic filaments has been measured by Henle,|| and found equal to 1 inch in 7½ minutes. The force of the motion was observed by the same physiologist, to be sufficient, easily to displace crystals of calcareous salts, ten times as large as the bodies of the spermatozoids. The body of the spermatozoid presents no movements, no contractions or dilatations.—The caudal filament alone is the seat of motion, and it continues to move when separated from the body. As to the character of the movements, Kölliker insists ¶ that their uniformity distinguishes them from the movements of infucory animalcules, which can vary their movements at will, or in accordance with their perception of external objects. On the other hand, the difference between the movements of the spermatic filaments and cilia, is not greater, he says, than would be expected to result from the one being fixed and the other altogether free.

One phenomenon which must be mentioned here, is the tendency of the spermatozoids to attach themselves to foreign bodies, such as flocculi of fibrin, or epithelium-scales.**

4. Wagner has corrected his statement, that strychnine and other narcotics instantaneously arrest the movements of spermatozoids.†† Solu-

* Appearances due to the same cause probably led Berres to imagine he saw a granular fluctuating mass, a canal filled with coloured matter, and a round vesicle, which might be a stomach or an ovary, in the spermatozoid of the human subject.—Oesterreich. Mediz. Jahrbücher, 1843, p. 141.

† Transactions of Zoological Society, February, 1846.

‡ Allgemeine Anatomie, p. 950.

§ Dujardin, Henle, Dalrymple, Pouchet, and Wagner. The last-named physiologist thinks the appearance at the root of the tail is the effect of commencing decomposition.

|| Allgem. Anat. p. 954. ¶ Op. Cit. p. 66 and p. 80.

** Henle, Kölliker.

†† The same observation has again been made by Prévost, and been advanced by him as an argument in favour of the opinion that the spermatozoids are independent animals. (L'Institut, No. 465.)

tions of these substances produce this effect only when they are so concentrated as to act chemically on the organic substance of the spermatic filaments.

Pure water at first accelerates the movements and then arrests them; at the same time causing the filaments to become twisted on themselves so as to form loops. The latter effect is produced in the most remarkable manner in the hair-shaped filaments of the invertebrata, and in less degree in the pin-shaped filaments of reptiles and Mammalia.*

5. Great additions have been made to our knowledge, of the process by which the spermatic filaments are formed, and the theory of their development has been much simplified. Kölliker, the most successful labourer in this field, proposed in 1841,† the law "that the seminal filaments are developed *either within cells, or by the transformation of cells,* which are formed in the testes at the time of puberty or of heat; the processes of development being analogous to those by which other elementary parts of animals are developed." And he referred the modifications of these modes of development to the following types.

Type I. Each spermatic filament is produced from a single cell by the elongation of the cell itself.

Type II. An entire fasciculus of filaments is produced from each cell, by this first assuming the cylindrical form and then becoming resolved into filaments.

Type III. A fasciculus of many filaments is formed *within* the cavity of a large cell.

Type IV. Each filament is formed *within* a separate cell.

Type V. The filaments are developed in fasciculi from finely granular cells, by the component granules of the cells coalescing in linear series, so as to form fibres, which then increase in length.

Only the third and fourth of these types were observed by Kölliker in the vertebrate classes of animals. The third type was, in fact, the mode of development of spermatozoid discovered by Wagner in birds.‡ The fourth type was discovered by Kölliker in the guinea-pig and mouse. The first stage in the process here observed by him, was the existence of large cells varying from $\frac{1}{166}$ to $\frac{1}{50}$ of a line in diameter. The smaller of these cells contained one or two granulated cellules; the larger cells filled with similar cellules. These granular cellules measured from $\frac{1}{285}$ to $\frac{1}{200}$ of a line in diameter. They were set free by the solution of the large parent cell, and then within each of them a spermatozoid made its appearance, the granules previously contained in the cellule disappearing at the same time. The body of the spermatozoid seemed to be formed by the coalescence of a large number of the granules. The

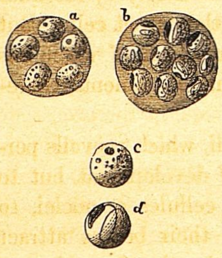
* Wagner's Physiologie.

† Beiträge zur Kenntniss der Geschlechts-verhältnisse und der Samenflüssigkeit wirbel-loser Thiere. Berlin, 1841, p. 53.

‡ See pp. 1475–6 of Müller's Physiology.

filament was coiled up, and in close contact with the inner surface of wall of the cellule (see figure 3). Wagner * confirmed Kölliker's discovery of this mode of development of spermatozoid, and stated that it prevailed in most, if not all mammalia, and likewise in many birds and reptiles. Henle ‡ afterwards conjectured that the third and fourth types of development admitted by Kölliker were essentially identical, that the globules seen by Wagner in the large cells of the semen of singing birds, previous to the appearance of the spermatozoids in those cells were really cellules, in each of which a spermatic filament was developed, and that the only difference between the process in this case, and that discovered by Kölliker in the guinea-pig and mouse was, that in the former the cellules are dissolved, and the filaments set free, the parent cell still remaining entire, whereas in the latter case the parent cell perishes first.

Fig. 3.†



This conjecture of Henle has been verified, in some measure, by observations of Dr. Martino, of Naples,§ on the development of spermatozoids in rays and torpedos, but more completely by Kölliker himself, who, in a second memoir,‖ has adduced a large body of evidence in support of the view that the development of the spermatic filaments *within* cells is the universal law. Kölliker believes that in those cases in which (as in the Types I., II., and V. described in his earlier work) spermatic filaments or spermatozoids appear to be formed by the lengthening out and transformation of the cells themselves, the process really consists in the formation of filaments, singly or in fasciculi, *within* the cells, although in many cases the minute size of the cells, and, in some cases, their opacity, render it extremely difficult, or even impossible, to determine the fact absolutely. In all the vertebrate classes, however, except the cyclostomatous fishes, and in many invertebrate animals (insects, arachnoids, cephalopods, and many gasteropods), he has distinctly observed the development of the spermatic filaments within the spermatic cells; and he has further ascertained with certainty in all these animals, insects exeepted, that each filament is formed singly within one of the smaller vesicles or cellules,

* Physiologie, p. 24.

† This figure is taken from Kölliker's more recent memoir, "Die Bildung der Samenfäden." It represents the development of the spermatozoids of the Rabbit. *a.* A parent cell or cyst, with five cellules or nuclei. *b.* A parent cell with ten cellules, each of which contains a spermatic filament. *c.* A free cellule or nucleus, with a nucleolus and granules, more highly magnified. *d.* A cellule in which a spermatic filament is seen, the granules having disappeared.

‡ Allgemeine Anatomie, p. 960.

§ Ann. des Sci. Natur. 1846, p. 297.

‖ Die Bildung der Samen-fäden in Bläschen. Nurenburg, 1846.

included in the cavity of the parent cell; so that the process is in all essentially the same as that already described as occurring in mammiferous animals. The smaller vesicles, within each of which a filament is formed, and which sometimes exist singly within the larger cells, but more frequently are multiple, were termed by Henle, and formerly by Kölliker himself, cellules, and the enclosing cell was termed the parent cell. But Kölliker now regards the enclosed vesicles as nuclei, each of which has generally, he says, one or two nucleoli. The spermatic filaments, therefore, according to Kölliker, are formed within nuclei.

The appearance of spermatozoids united in fasciculi, which prevails perhaps in all animals, is not owing to their mode of development, but to their tendency, when set free from their formative cellules or nuclei, to arrange themselves thus; a tendency shewing that their bodies attract each other in the same way that blood-disks do in the formation of *rouleaux*. The fasciculi are formed within the parent cell, when this remains entire after the nuclei or cellules are dissolved; in other cases they are formed in the seminal fluid by the union of spermatozoids which have been wholly set free by the solution of both parent cell and nuclei.

6. The opinion that the spermatozoids are not independent living animals, but merely elementary parts of the organism in which they exist, is becoming generally adopted. Kölliker, Henle, and apparently Wagner, also, as well as Dujardin, take this side of the question.

Besides the arguments adduced by Professor Müller * in support of this opinion, Kölliker urges the narrow limits within which their varieties of form are comprised, a circumstance distinguishing them from Entozoa, and the character of their movements; † but lays especial stress on the fact that they are normal and essential constituents of the seminal fluid. " It cannot be conceived," he says, " that a fluid so important and so strictly vital, in the sense that the blood is vital, which conveys the physical, and even the mental properties of the animal, should be the nidus for the development of foreign and independent beings, whether produced from germs introduced from without, or the result of equivocal generation; and should afford nourishment to these foreign beings while it still retains its own high endowments. And it is still less conceivable that these independent creatures should be the normal, and, indeed, essential parts of such a fluid."

We have already seen that the argument in favour of the spermatozoids being independent animals, drawn from the action of narcotics on them, is not well-founded.

Supposing them to be merely elementary particles of the organism in which they exist, their movements must be ascribed to a cause analogous to those which produce the vibrations of cilia, and the peculiar movements of the sensitive plant.

* Physiology, p. 1477.

† See *ante* p. 40.

7. Function of the spermatozoids.

That the spermatozoids are normal and essential elements of the semen, is evident from many facts. These facts are the presence of such particles in the seminal fluid of all classes of animals, (the Infusoria being the only class in which they have not been discovered); the large proportion they constitute in the bulk of the seminal fluid, (the fully formed semen consisting almost wholly of a mass of spermatozoids); their close connection with the states of puberty and of heat in the males of all animals (they being first formed at the age of puberty in the human subject, and being periodically produced at each time of heat in animals, while in the intervals they disappear); the presence of these spermatozoids on or about the ova which are observed immediately after fecundation, (Barry, Bischoff, Pouchet, and other recent observers,) and, lastly, the apparently conclusive proof obtained by Prevost,* who filtered frog's semen by means of a bladder, and found that the filtered fluid had not the power of impregnating ova, while the spermatozoids, which did not pass through the filter, still retained the fecundating property.

Bischoff and Valentin, however, think that the fecundating principle itself is contained in the fluid part of the semen, which passes by imbibition through the zona pellucida; and that the function of the spermatozoids is two-fold, first, by their energetic movements to act as carriers of the seminal fluid to its destination at the ovum; and, secondly, by the same active movements, and probably also by some chemical quality, to maintain in its integrity the due mixture and composition of the liquor seminis: acting, in this latter respect, a part somewhat analogous to that performed by the corpuscles of the blood towards the liquor sanguinis.

OF THE DISCHARGE OF OVA FROM THE OVARIES.†

These processes have become the subjects of much discussion during the last few years, and the following questions relating to them have been especially examined.

1. What determines the discharge of ova from the ovary?

2. Is the presence of a corpus luteum in the ovary a sure evidence of previous impregnation?

3. What is the nature and purpose of the function of menstruation?

Respecting the first two questions, the opinions of physiologists have for a long period been extremely various and unsettled. Of late years, however, the opinion has been gaining ground that the discharge of ova from ovary is independent, not only of impregnation, but also of sexual inter-

* L'Institut, 1840, No. 362.

† Book viii. sect. ii. chap. v. p. 1481, of Müller's Physiology.

course, and is closely connected with the phenomena of heat in animals, and menstruation in the human female. Bischoff* and Raciborski,† have at length obtained conclusive evidence of the correctness of this view, as far as it regards mammiferous animals. They have also contributed, with many other contemporary writers, to establish the important fact that *corpora lutea* may be formed under other circumstances than those of impregnation.‡

The following is the law of generation which M. Bischoff lays down as applicable both to Mammalia and to man:—

"The ova formed in the ovaries of the females of the human species and mammiferous animals, undergo a periodical maturation, quite independently of the influence of the male seminal fluid. At these periods, known as those of 'heat' or the 'rut,' in animals, and 'menstruation' in the human female, the ova which have become mature disengage themselves from the ovary and are extruded. Sexual desire manifests itself in the human

* Comptes Rendus, 17 Juillet, 1843. Beweis der von der Begattung unabhängiger periodischen Reifung und Loslösung der Eier, Giessen, 1844. Translated by Mr. H. Smith, in Med. Gaz., Jan. 3, 17, &c., 1845

† Comptes Rendus, Séance du 17 Julliet, 1843; and De la Puberté et de l'age critique chez la femme et de la Ponte périodique, 8vo. Paris, 1844, p. 405, *et seq.*

‡ Malpighi, and many other Italian writers after him, asserted that the ova were not only formed, but also discharged from the ovaries, *previous to*, and *independently of*, *fecundation or the union of the sexes;* both their formation and their discharge being effected by the agency of corpora lutea, which these writers regarded as glands produced in the ovaries, even of virgin animals, for that purpose. The ova, when discharged, became impregnated, Malpighi believed, either in the Fallopian tube, or in the uterus. (Malpighi, Opera Omnia, 4to. Lugd. Batav., 1687, p. 222-224).

These views were opposed by Haller, who maintained that the ova of quadrupeds and the human female, are separated from the ovaries, and corpora lutea formed, only in consequence of impregnation; and the weight of Haller's opinion had caused Malpighi's theory, and the facts he announced to be neglected, at all events, in this country, when, in 1817 Sir Everard Home re-produced them as new discoveries. (Lectures on Comparative Anatomy. vol. iv. p. 297. Philos. Transactions, 1817, p. 25, 1819, p. 59.) Sir E. Home gave Malpighi's theory a more complete form, stated the facts on which it was based more precisely, and also connected the discharge of the ova with the phenomena of heat and menstruation, which Malpighi had not done.

Four years later Dr. Power published an Essay on the Nature and Causes of Menstruation, (Essays on the Female Economy, London, 1821,) in which he endeavoured to shew from analogical reasoning and the facts observed by physiologists; 1st. that Menstruation is an effect of the state of orgasm which arises in the ovaries every month; 2nd. that this state of the ovaries is connected with the maturation of the ova, which successively reach maturity after intervals of a lunar month; 3rd. that the mature ovum, if impregnation does not take place, usually perishes within the ovarium, and is removed by the process of absorption; but 4th. that the vascular action in the ovary may, independently of sexual intercourse, be sufficiently great to cause the expulsion of the ovum, and 5th. that in this case a corpus luteum will be formed as a cicatrix of the ruptured Graafian vesicle.

The discovery of the unimpregnated ova in the Graafian follicles of mammiferous animals, by Von Baer, in 1827, afforded a basis for more accurate investigations of the phenomena of impregnation, and of the circumstances under which ova may be discharged from the ovary.

female with greater intensity at these periods, and in the females of mammiferous animals at no other time. If the union of the sexes takes place, the ovum is fecundated by the direct action of the semen upon it. If no union of the sexes occurs, the ovum is nevertheless extruded from the ovary, and enters the Fallopian tube; but there perishes. The relation in respect of time between the extrusion of the ovum, and its fecundation by the semen, may vary to a certain extent; and the limits of this variation seem to be different in different animals. The seminal fluid may have time to reach the ovary before the ovum is extruded; or the ovum may escape first, and afterwards meet the semen in the Fallopian tube. But the fecundating influence of the semen must be exerted on the ovum before it has quite passed through this tube, otherwise development will not take place; for the development of the ovum commences in the Fallopian tube. It is only at the time of the periodical maturation of the ova that sexual union can have impregnation for its result." *

M. Bischoff also maintains, in common with other recent writers, that the discharge of ova at the periods of heat or menstruation, always gives rise to the formation of corpora lutea.

It may be useful to examine the evidence on which these views respecting the maturation and discharge of ova, and the formation of corpora lutea are based.

Ova are matured and discharged from the ovary independently of impregnation and sexual intercourse; and their discharge takes place periodically, namely, at the periods of heat in animals, and menstruation in the human female.

With respect to *mammiferous animals*, lower than man, these statements are undoubtedly correct. In the first place, there is ample evidence to

Nevertheless, until very recently, but little addition was made to our knowledge on these subjects. The theory of Malpighi, in the modified form which it received from Sir E. Home and Dr. Power, was reasserted with more or less distinctness, by Dr. Lee, in 1834 (Cyclopedia of Practical Medicine, Art. Ovary.), M. Gendrin, in 1839 (Traité Philosophique de Médecine Pratique, tom. i. p. 28, *et seq.*), Dr. W. Jones, in 1839 (Practical Observations on Diseases of Women, London, p. 157, *et seq.*). M. Negrier, in 1840 (Recherches Anatom. et Physiol. sur les Ovaries, Paris), Dr. Paterson, in 1840 (Edinburgh Med. and Surg. Journal, vol. 53, p. 62), Mr. Girdwood (Lancet, 1842-1843, vol. i. p. 825), and M. Pouchet, in 1842 (Théorie Positive de la Fécondation, Paris).

But although facts of great interest had been adduced by many of these authors, in support of their theory, and had been detailed by them with more accuracy than by the earlier writers, yet these facts were not in their nature new, and were not generally received as conclusive proofs. M. Bischoff and M. Raciborski were the first to apply the light afforded by Baer's discovery to the elucidation of this subject, and to demonstrate the unimpregnated ovum of a mammiferous animal in the Fallopian tube, after its escape from the Graafian follicle. The observations of M. Bischoff and those of M. Raciborski, were published at the same time, but the descriptions given by the former are much the more detailed and precise.

* Beweis, &c., p. 4.

prove that in these animals, as in the lower classes, ova are discharged from the ovaries independently of the influence of the male.

Several experimenters Dr, Blundell,* Hausmann,† and Bischoff,‡ have observed that, when one oviduct, or one half of the uterus has been tied or divided in an animal previous to coitus, although fœtuses are subsequently met with only on that side on which the passage to and from the ovary remains free, yet ruptured ovarian vesicles, or corpora lutea, are found in *both* ovaries. And Dr. Blundell has shewn that the result, as regards the ovaries, is the same, if the vagina be divided near to the mouth of the uterus, so as completely to interrupt its canals, and to prevent the seminal fluid from reaching even the uterus, although, of course, no embryos are produced in this case. These experiments proved that Graafian follicles burst independently of the contact of the seminal fluid; but still they left room for the objection that the rupture of the follicles might have been caused by the excitement attending sexual connection. This objection, however, does not apply to the fact vouched for by many writers of high authority—Cruikshank, Sir E. Home,§ Paterson,|| Hausmann,¶ Raciborski,** and Bischoff,—and now almost universally admitted, that if mammiferous, which have been kept separate from the male, be killed during the period of heat, the Graafian follicles will be found either turgid and extremely vascular, or already burst and in various stages of conversion into corpora lutea.

All the foregoing observations were, however, defective inasmuch as they did not demonstrate the ova which had escaped from the ovaries. This deficient link in the chain of evidence has been supplied by M. Bischoff and M. Raciborski. The following is an abridged account of one of M. Bischoff's important observations.†† On the 18th and 19th of December, 1843, he remarked that a large bitch in his possession commenced to be in heat. He kept her closely shut up, and on the 23rd (having previously, on the 21st, ascertained that she was disposed to receive the male, though he did not permit coitus to take place) he cut out the left ovary and Fallopian tube, and closed the wound by suture. On examining the ovary he found that no Graafian follicles had yet opened, though four of them were much swollen, undergoing the changes preparatory to the discharge of the ova. Five days later he killed the animal and he now found that rupture of the follicles in the remaining right ovary had taken place. Four corpora lutea were well developed.

Bischoff now sought for the ova. Having carefully dissected the

* Medico-Chirurgical Transactions, vol. x. p. 254. Experiments on Rabbits.

† Ueber die Zeugung des wahren Weiblichen Eies. Hannover, 1840, p. 93.

‡ Beweis, p. 10-17.

§ Philos. Transact. 1817, 1819.

|| Ed. Med. and Surg. Journal, vol. liii. p. 64.

¶ Ueber die Zeugung des wahren Weiblichen Eies. p. 94, 95, and 96.

** Op. Citat. p. 376, *et seq.*

†† Beweis, p. 28.

Fallopian tube, extended it upon a wax tablet, and opened it with a pair of fine scissors, he found the four extruded ova, far advanced in the cavity of the tube; they were close together, at a distance of three inches (Paris measure) from the ostium abdominale. Three of these ova had the usual round form; the fourth had an anomalous shape. All had still the discus around the zona; but it was clear that the cells of the discus no longer retained their full normal appearance, but had already begun to undergo liquefaction. Similar observations were made by Bischoff on a sow and a rat. M. Raciborski also found an ovum in the oviduct of a bitch that had been kept, during the period of heat, separate from the male.

It is certain, then, that in mammiferous animals, as in the lower classes, ova are brought to maturity and discharged from the ovaries independently not only of the direct action of the semen, but also of the excitement attending sexual union. The following facts and considerations seem to render it almost as certain that this phenomenon of the maturation and extrusion of the ova takes place periodically; namely, at those times which are marked by the phenomena of heat or rut. Before the age of puberty, when the first period of heat occurs, no corpora lutea are to be found in the ovaries; but at this time they make their appearance, even though the animal should be kept separate from the male.* Then it is to be remarked, that in all the instances recorded with any degree of minuteness of Graafian follicles presenting the appearance of being recently ruptured, the animals were at the time, or had recently been, in heat; and that, on the other hand, there is no authentic and detailed account of Graafian follicles being found ruptured in the intervals of the periods of heat. Again, the fact that female animals do not admit the males, and never become impregnated, except at those periods, strongly confirms the idea that ova are discharged at no other times.

That the maturation and discharge of ova takes place normally at *every period* of heat, although it cannot be said to be proved, is at least in the highest degree probable. The instances in which the Graafian follicles have been found ruptured in animals in heat are already numerous; and it is generally admitted, even by authors who deny the bursting of the Graafian follicles, or at least the formation of true corpora lutea except as consequences of impregnation, that at every period of heat in animals the ovaries become turgid with blood, and that a certain number of vesicles at the same time enlarge and become very vascular.†

It has been shown, too, by Dr. Barry,‡ as well as by Bischoff in his earlier researches, that the ova in those vesicles which are enlarged at the periods of heat, themselves present certain changes in their size and structure which

* Sir E. Home, Phil. Transactions, 1819.

† Cruikshank, Phil. Trans. 1797. Hausmann, Op. Cit. p. 73. Paterson, Edin. Med. & Surg. Journal, vol. liv. pp. 394 and 401.

‡ Phil. Trans. 1832, Part ii. p. 310, par. 125.

may be regarded as signs of their maturity. And experiments, such as the one on the bitch just quoted from Bischoff, seem to show that the turgid state of the Graafian follicles is preparatory to their spontaneous rupture and the discharge of the matured ova.

It is almost impossible to doubt, therefore, that in mammiferous animals every period of heat is normally accompanied, not merely by a vascular turgescence of the ovaries and their Graafian follicles, but also by the maturation of a certain number of ova, and their extrusion from the follicles which contained them; and that all this takes place independently of sexual intercourse.

We have now to inquire whether the *human* female is subject, in this respect, to the same law as the female of other mammiferous animals; whether ova are discharged from the human ovary under any other circumstances than those of impregnation; and, supposing this first question to be answered in the affirmative, whether the maturation and discharge of ova occurs periodically at the epochs of menstruation.

Respecting the former of these questions scarcely any doubt can be entertained. Ovarian follicles recently ruptured have been seen so frequently, and by so many independent observers,* in the ovaries of virgins or women who could not have been recently impregnated, that it must be regarded as certain that the follicles of the human ovary do burst from other causes than impregnation or sexual connexion; and although it is true that the ova discharged under these circumstances have not hitherto been discovered in the Fallopian tube, yet analogy forbids us to doubt that in the human female, as in the domestic quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova. Whether the maturation of ova and the discharge of them from the ruptured follicles in the human female takes place periodically at the epochs of menstruation, cannot, at present, perhaps, be decided with absolute certainty; but the evidence in favour of the affirmative of the question greatly preponderates.

In the first place, it is agreed by all authors who have touched on the point, except Dr. Ritchie, that no traces of follicles having burst are ever seen in the ovaries before puberty or the first menstruation. Secondly, all the writers who have described the particulars of the cases in which the ovarian follicles were found burst independently of sexual intercourse, with the exception again of Dr. Ritchie, state that the women were at the time menstruating, or had very recently passed through the menstrual state.

* Sir E. Home, Phil. Trans. 1817. Dr. Blundell, Physiol. and Pathol. Researches, 1824, p. 56, Med. Chir. Trans. 1819, p. 268. Dr. Lee, Cyclopedia of Medicine, Art. Ovary. 1834; Lectures on Theory and Practice of Midwifery, 1844. Gendrin, Méd. Pratique, t. i. p. 28. W. Jones, Practical Observations on Diseases of Women, 1839, p. 157. Paterson, Edin. Med. and Surg. Journal, vol. liii. Laycock, Medical Gazette, 1840. Devaix, Gazette Médicale. Raciborski, Bischoff. Girdwood, Dr. Ritchie, Pouchet, loc. citat. M. Serres, Comptes Rendus, Nov. 18, 1844.

Thirdly, although in women, sexual connexion is not confined to these periods, yet it is an old observation, confirmed by the experience of some eminent modern accoucheurs, and by the results of inquiries instituted by M. Raciborski, that conception is more likely to occur within a few days after the cessation of the menstrual flux than at other times: and hence the distinguished obstetrician, Naegeli, is accustomed to reckon the duration of pregnancy at nine months and eight days from the last menstrual period, and in normal cases has, he says, never been wrong. These are strong grounds for believing that the discharge of ova is confined to the periods of menstruation.

The number of facts at present collected are insufficient to establish it as a law that an ovum is discharged from the ovary of the human female *at every normally developed period of menstruation.* Yet it must be observed that although the diseases causing death must, in the majority of instances, disturb the function of the ovaries, and prevent the extrusion of the ovum, yet to each of those inquirers who have been on the watch for such cases, several instances of ruptured follicles in menstruating woman have occurred within a short space of time. And the fact that the ovaries of the human female become turgid and vascular at the menstrual periods, as those of animals do at the time of heat, strongly favours the opinion that the generative system of the human female is subject to the almost universal law of the periodical discharge of ova.*

The discharge of an ovum always gives rise to the formation of a corpus luteum.

This is the statement of M. Bischoff. But most of the recent writers

* Dr. Ritchie, however, adduces some observations, which, if confirmed, would shew that the operation of this law is much modified in the human subject. He states that ovarian follicles are found ruptured even before the commencement of menstruation, as well as during its subsequent suspension, whether this arises from normal causes or a disordered state of the system. He admits, however, that the full development of the ova and the Graafian follicles is generally, though not necessarily, associated with menstruation, (Contributions, second series, part ix. Med. Gaz. vol. xxxvi. p. 811,) and that only those of follicles which burst at or about the time of menstruation, undergo further organic development, or changes in their coats. (p. 982.) The openings, too, in the peritoneum over the ovarian follicles of the amenorrhagic or non-menstruating female, Dr. Ritchie states, are punctiform, while in the menstruating female they are uniformly linear or crucial and of much larger size. This difference he ascribes to the greater activity of the ovaries in menstruating, than in other women. (p. 325.) Dr. Ritchie also maintains that menstruation may occur several successive times without the evolution of an ovum; founding this statement on his examination of the ovaries of women who had menstruated regularly. (p. 940.) But this, it is obvious, is no formidable objection to the theory that the extrusion of ova is connected with the function of menstruation. For the organic excitement and vascular turgescence of the ovaries, on which menstruation certainly depends, may have been sufficient to determine the occurrence of the latter function, but yet, from some cause or other, inadequate to produce the rupture of an ovarian follicle. In some cases, too, it may, and in all probability, does happen, that ova are matured, and the follicles prepared for bursting, yet the discharge of the ova is prevented by a thickened state of the peritoneal covering of the ovary.

on the subject, Paterson, Lee, Ritchie, Raciborski, Deschamps, and Renaud maintain, at all events as regards the human female, that a true and fully formed corpus luteum is met with only where an ovum has been impregnated; and, consequently, that such a body is a sure evidence of previous impregnation. Most of these writers lay great stress on the distinction to be drawn between true and false corpora lutea.

In order the better to judge of the value and correctness of their views it will be well in the first place to inquire what is the structure and mode of growth of a corpus luteum formed during pregnancy in mammiferous animals as well as in man.

The corpus luteum of mammiferous animals when fully formed is a roundish solid body, of a yellow or orange colour, and composed of a number of lobules which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance; the delicate processes given off by this white mass passing as septa between the different lobules of the yellow body. Very often in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian follicle, appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

It is an important fact, that the development of the *corpus luteum* commences before the rupture of the Graafian follicle. The follicle which is about to burst and expel the ovum, becomes highly vascular and also opaque; and *immediately* * before the rupture takes place, its walls appear thickened on their interior by a reddish, glutinous or fleshy substance. Immediately after the rupture the inner layer of the wall of the follicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and soon red fleshy mammillary processes grow from it, and gradually enlarge till they nearly fill the follicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

The corpus luteum of the human female differs from that of the domestic quadruped, in being of a firmer texture and having more frequently a persistent cavity at its centre, and in the stelliform cicatrix which remains in the cases where the cavity is obliterated, being proportionally of much larger bulk.

The following are the more obvious phenomena of its formation:— First, the Graafian follicle which is about to discharge its contents, becomes very vascular, then its walls lose their transparency and a very thin

* The time, according to Bischoff's observation, (Entwickelungs-geschichte, p. 32,) must be very short.

layer of soft yellowish matter appears in them.* When the follicle bursts, this yellowish deposit increases. It does not, however, usually form mammillary growths projecting into the cavity of the follicle, and never protrudes from the orifice, as is the case in other mammalia. It maintains the character of a uniform, or nearly uniform layer, which is thrown into wrinkles in consequence of the contraction of the external tunic of the follicle. After the orifice of the follicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated; in the latter case, merely a white stelliform cicatrix remaining in the centre of the yellow body.

In some mammalia as well as in the human subject, an effusion of blood generally takes place into the cavity of the Graafian follicle at the time of its rupture, but in the latter it is more constant and in greater quantity than in the former. The effused blood, however, has in no case any share in forming the yellow body. It gradually loses its colouring matter and acquires the character of a mass of fibrin. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorized fibrin forms a membraniform sac, lining the corpus luteum. At other times the serum of the blood is removed, and the fibrin constitutes a solid stelliform mass.

There has been much difference of opinion as to the origin of the growth which forms the yellow body. But most of the modern writers of high authority who appear to have examined the corpora lutea in the earliest stage of their growth, with the aid of the microscope, Valentin, R. Wagner, Bischoff, Raciborski, and Zwicky, corroborate the statements of Haller and Von Baer, that the growth arises from the inner surface of the follicle; and shew that it is, in fact, the result of an increased development of the cells forming the membrana granulosa which lines the internal tunic of the Graafian follicle.

The mode of formation of the corpus luteum in the cow and sow has been made the subject of a minute microscopic investigation by Zwicky, the accuracy of which, in all important points, has been verified by the writer.

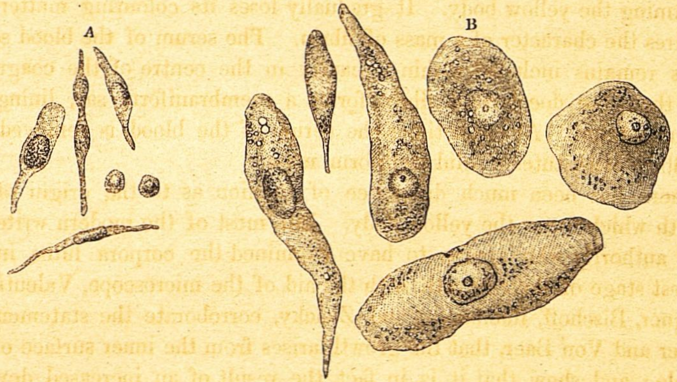
The Graafian follicle, according to Zwicky, has really but one tunic or theca, which, although separable into two layers, is throughout composed of the same elements; namely, granular nucleated cells, in part round and varying in size, and in part becoming elongated into fibres (fibro-cells). (Fig. 4, A.) The conversion of the cells into fibres is further advanced in proportion as they are nearer to the outer surface of the theca, where they can no longer be distinguished from the fibres forming the stroma of the ovary. Floating in the fluid contents of the follicle, are granular nucleated cells, round, ovate, or fusiform, and similar to those forming the innermost stratum of the theca.

* Negrier, Ritchie.

When the follicle enlarges at the time of heat, and before the escape of the ovum, the cells floating in the fluid, and those forming the inner surface of the theca, undergo a twofold transformation. Some merely become elongated and present the various stages of transition into fibres, while others become much enlarged in all directions, acquiring four or five or even ten times their original diameter; their nuclei at the same time attaining double their former size, and presenting very distinct nucleoli.

These enlarged cells are marked with granules of fatty matter of yellow colour (fig. 4, B), some of these granules are contained within the cells, but others are adherent, M. Zwicky thinks, to their outer surface while the greater part lie free in the interstices of the cells. When the large cells have attained their full size they either burst or become elongated, so as to form fibres which are distinguished from the fibres resulting from the direct

Fig. 4.



transformation of the smaller cells, by their breadth, the large size of their nuclei, and the presence of fat granules in them. Cells presenting all these varieties of form may be found in the fully formed Graafian follicle immediately previous to the escape of the ovum; some floating in the fluid contents, others forming plicæ or villi on the inner surface of the theca.*

In a follicle from which the ovum has recently escaped, the theca is thicker, and its inner strata are of a loose texture and red colour, and consist chiefly of the large cells above described, mixed with some small nucleated cells in part elongated into fibres, a few bodies resembling the nuclei of the large cells, and numerous free, yellow, or orange coloured fat granules. The external strata of the theca present no change from their early condition.

* It may be doubted whether these large cells are not altogether new formations. M. Zwicky gives no very satisfactory evidence of their being even in part developed from the small cells of the immature Graafian follicle.

The further progress in the formation of the corpus luteum consists in the continued growth, or as it were vegetation, of the internal strata of the theca towards the cavity of the follicle; this growth of the theca being dependent on the continued increase in size of its component cells, and the development of new cells of the same kind.

In the fully formed corpus luteum the nucleated fibres resulting immediately from the transformation of the smaller cells are disposed in fasciculi which traverse the mass, and form, as it were, a frame-work, apparently destined to support the nutrient vessels. The large cells and fibro-cells distinguished by the fat granules they contain, seem to have no regular arrangement.*

Respecting the mode of development of the human corpus luteum very various opinions have been held; some writers, as Dr. Montgomery, Dr. Paterson, Dr. Ritchie, and Dr. Frank Renaud,† maintaining that the yellow substance is deposited between the two tunics of the Graafian follicle; others, as Dr. Lee, asserting that the growth of the yellow substance takes place external to both tunics: while most of the German and French writers assume, and M. Raciborski ‡ states, from direct observation, that as in the mammalia, so in the human subject, it is the inner surface of the tunic that produces the yellow body. That the last view is the correct one the writer is satisfied, from the results of the examination of many human corpora lutea in various stages of their growth. For in several which were in an early stage, no membrane whatever could be demonstrated on the interior of the layer of yellow substance, and a particle taken from its inner surface was found on microscopic examination to consist of the elements already described as forming the corpora lutea in domestic quadrupeds. Where a membrane did exist on the interior of the yellow substance it was found to be composed of elements very different from those which constitute the inner strata of the tunic of the Graafian follicle,—it was composed not of granular nucleated cells, nor of fibro-cells, but of the delicate non-nucleated fibres into which the fibrin of the blood or liquor sanguinis is transformed subsequent to its coagulation.

The microscopic elements of the fully formed corpora lutea are essentially the same in the human subject as in the domestic animals.§

* The corpus luteum of the sow and cow, is, according to Zwicky, never entirely re-absorbed. But, by the rupture of some of the larger cells, the transformation of others into fibro-cells, and the subsequent absorption of the greater part of these fibro-cells, it is at length reduced to a small mass, consisting of imperfectly-formed fibres of cellular tissue, mixed with dark yellow fat, the quantity of which is proportionally much greater in corpora lutea which are undergoing diminution in size, than in those which are still at the maximum of their development.

† Cormack's Monthly Journal of Medical Science, vol. v. 1845, p. 600.

‡ Bulletin de l'Acad. Roy. de Médecine, 15 Oct. 1844.

§ This statement is founded on the writer's own observations, as well as on the descriptions of Raciborski and Renaud.

Having thus learned the structure and mode of formation of the corpora lutea which are seen in impregnated animals we have now to enquire whether such bodies are always produced as a consequence of the rupture of Graafian follicles, and the discharge of their ova. This question must undoubtedly, with some limitation, be answered in the affirmative, as far as it regards quadrupeds in the state of heat. For even if the statements of the older anatomists, who speak of having found corpora lutea in unimpregnated animals, were left out of consideration, the more recent observations of Sir E. Home, Dr. Blundell, M. Raciborski, and M. Bischoff, would render it certain that the extrusion of ova from the Graafian follicles of animals in heat, is attended with the formation of corpora lutea even when the extruded ova do not become impregnated. In the figures, given by Sir E. Home * and M. Bischoff,† of corpora lutea formed under these circumstances, it is evident that the growth of the yellow substance has proceeded to such an extent as to protrude from the orifices of the ruptured follicles, after filling their cavities. These are certainly corpora lutea which could not be distinguished from corresponding bodies of the same stage of development in the ovaries of impregnated animals. In the impregnated animal, however, the corpus luteum continues to increase in size after the orifice in the follicle has closed; and whether this is the case in animals which are not impregnated is doubtful. It is probable that if the ova have not been fecundated, the state of orgasm of the ovaries and Graafian follicles, which arose during the condition of heat, subsides, and that the corpora lutea then, instead of continuing to grow, quickly shrivel and disappear. For if it were not so, if the corpora lutea attained their full size in unimpregnated animals, the ovaries of those animals in which the period of heat recurs after short intervals, would constantly be found to contain fully formed corpora lutea; and this is not the case.

With regard to the human female the limitations with which the rule may be admitted are greater. There is reason to believe that under normal circumstances the rupture of a Graafian follicle and the discharge of an ovum at the period of menstruation is attended with that change in the tunic of the follicle which constitutes the first step in the formation of the corpus luteum. For amongst the descriptions given by writers ‡ of ruptured Graafian follicles found in virgins and other menstruating women who could not have been recently impregnated, there are several in which it is distinctly stated that a layer of yellow substance existed in the walls of the follicle; and in other instances, bodies resembling in structure the corpora lutea of pregnant women have been found in the ovaries of females who had menstruated at some distance of time, and who had not been pregnant.§

* Lectures on Comparative Anatomy, vol. iv. † Ann. des Sc. Nat., 1844.

‡ Dr. Lee, Dr. Paterson, Dr. Ritchie, Renaud, op. citatis.

§ Dr. Ritchie's case. x. part i. sec. ii. Medical Gazette, and Dr. Blundell's case, seem to have been unquestionably of this nature.

But the layer of yellow matter in the recently ruptured follicle was in such cases very thin, and the yellow body though in all other respects similar to the corpus luteum of a pregnant woman, was of much smaller size. It appears, therefore, that the development of the corpus luteum does not proceed so far in the menstruating woman as in animals in heat. The reason of this inferior degree of development of the corpus luteum in the woman, in comparison with that in quadrupeds, is easily conceivable; the excitement of the ovaries and the whole sexual system being undoubtedly far greater in the female quadruped in the state referred to than it usually is in the human female at the period of menstruation.* The degree of vascular excitement in the generative organs attending the process of menstruation is moreover liable to great variety. It may sometimes be only just sufficient to cause the rupture of the follicle, and not adequate to the production of yellow substance by an organic change in its tunic. In this way we may account for the fact that in the greater number of the descriptions of ruptured Graafian follicles observed in unimpregnated women, no mention is made of the existence of a yellow deposit in the walls of the follicle. The follicles thus destitute of yellow substance when collapsed would form the *corpora albida* of Dr. Ritchie. On the other hand we must admit that when great excitement attends menstruation the formation of the corpus luteum may go on more rapidly and continue for a longer period, and that under these circumstances the resulting yellow body may be of considerable size.

If, in addition to the foregoing facts and considerations, the varieties in size of the corpora lutea formed during pregnancy are borne in mind, it will be seen that cases can seldom occur where the mere presence of one of those bodies can be taken as a proof of previous impregnation. The following practical rules, however, seem to be deducible from the facts detailed.

1. A corpus luteum, in its earliest stage (that is a large vesicle filled with coagulated blood, having a ruptured orifice, and a thin layer of yellow matter in its walls), affords no proof of impregnation having taken place.

* The fact is announced by M. Raciborski, (Acad. de Médecine, Séance du 15 Oct. 1844. Gaz. Med. Oct. 19, 1844,) as a deduction from his experiments and dissections, in the following terms: "In the females of most of our domestic animals, whether they have or have not had sexual intercourse with the males, the expulsion of the ovule is always followed by the formation of a corpus luteum, a fleshy mass, of a yellow or reddish colour. It is different, however, with women. If the expulsion of the ovule, at the period of menstruation, is not followed by conception, the granulations on the inner surface of the Graafian follicle increase in size; but this activity of nutrition soon ceases after it has produced a thin membrane, of a yellow colour, lining the proper membrane of the follicle, and enclosing a cavity in which traces of a clot of blood may be found. If, on the contrary, conception should take place, the elements of the granular layer of the follicle continue to increase in number and volume, until, in a short time, they form a mass of sufficient volume to fill the whole cavity of the follicle."

2. From the presence of a corpus luteum, the opening of which is closed, and the cavity reduced or obliterated, only a stellate cicatrix remaining, also no conclusion as to pregnancy having existed or fecundation having occurred can be drawn, if the corpus luteum be of small size, not containing as much yellow substance as would form a mass the size of a small pea.

3. A similar corpus luteum of larger size than a common pea, would be strong presumptive evidence, not only of impregnation having taken place, but of pregnancy having existed during several weeks at least; and the evidence would approximate more and more to complete proof in proportion as the size of the corpus luteum was greater.

What is the nature and purpose of the function of menstruation?— This question has reference chiefly to the theoretical views deduced from the facts detailed in the preceding pages. Bischoff, and the other physiologists, who believe that ova are normally expelled from the ovary at the periods of heat in animals, and of menstruation in the human female, regard those two states, heat and menstruation, as perfectly analogous. The essential character of both, according to their view, is the maturation and extrusion of ova. In both there is a state of active congestion of the sexual organs, sympathizing with the ovaries at the time of the highest degree of development of the Graafian follicles; and menstruation is only the crisis of this state of congestion.*

This theory is principally based, first on the long admitted fact that the changes which take place in the female system at the time of puberty, and the periodic recurrence of menstruation from that epoch to the end of the fruitful period of woman's life, are dependent on the presence and healthy condition of the ovaries; secondly, on the fact, which has also long been known, that at every period of menstruation, as at every period of heat in female animals, a vascular turgescence of the ovaries takes place; and thirdly, on the more recently alleged fact, that at the period of menstruation in women, as well as at the time of heat in animals, ova are normally extruded from the ovaries.

The two main arguments used by those physiologists who have denied the existence of an analogy between heat and menstruation, are that the heat is characterized by an excited state of sexual desire in the female, and by the occurrence of coitus at that time exclusively, while the menstruating woman has no strong feeling of sexual desire, and is repulsive to the male sex; and that a true menstrual discharge of bloody fluid is not observed in animals.

* Raciborski, Op. Cit. p. 446. See also Dr. Lee's remarks in Cyclop. of Med. Art. Ovary; and M. Pouchet's, in his work, Théorie Positive de la Fécondation, p. 87, *et seq.*; and more recently in an enlarged edition of this work under the title of Théorie Positive de l'Ovulation Spontanée et de la Fécondation des Mammif. et de l'espèce humaine. Paris, Baillière, 1847, p. 227, *et seq.*

In answer to the first of these arguments, Bischoff says, that "no such essential difference between the conditions of heat and menstruation exists. The female quadruped at the commencement of the state of heat appears to be in a state of general suffering, and will not admit the caresses of the male; it does not seek the coitus until this first stage of the heat is passed. The human female, on the other hand, at the time of the cessation of menstruation feels herself unusually well, and is more than ordinarily disposed for sexual connection. So that there is in this respect a most complete accordance between the two functions." * M. Bischoff might have added, that the less marked development of the sexual feeling in woman at the periods of menstruation, than in female quadrupeds at the periods of heat, corresponds with a fundamental mark of distinction between man and the brute. In animals it is natural that the instinct inducing the act of coitus, should be strongly developed at the times when that act may have for its result the fecundation of ova, and that the instinct should not exist at other times when no ova are prepared for fecundation. In women such a strong development of the sexual feeling, and aptitude for sexual intercourse, exclusively at particular times, would have been in contradiction to the freedom of will and self-command which characterizes the human species.

With regard to the argument founded on the hemorrhagic nature of the menstrual discharge in women, Raciborski † remarks that this discharge is not the essential phenomenon of menstruation—that women have become pregnant who had never menstruated; that although the discharge attending the heat in quadrupeds is in most cases simply mucous, yet in many of them it is occasionally bloody, and in some, nearest to man, consists chiefly of blood; ‡ and, on the other hand, that although the menstrual discharge in women is essentially bloody, yet at the commencement and end of menstruation, the blood is mixed with an increased flow of mucus, and with epithelium thrown off from the mucous surfaces of the sexual passages.

Assuming, now, that the theory of the discharge of ova periodically at the times of menstruation, and exclusively at those times, is correct, as it certainly is highly probable, the question next presents itself,—how long after the extrusion of the ovum from the ovary, or how long after the cessation of the menstrual discharge is fecundation possible. The passage of the ovum from the ovary to the uterus occupies, M. Bischoff says, three days in the rabbit, and four or five days in ruminants, and, therefore, probably eight or ten days in the human female. M. Bischoff believes that the ovum escapes from the Graafian follicle at the time when the menstrual discharge is about to cease, and he is of opinion, that in order to be fecundated, it must be acted on by the semen while it is in the Fallopian tube. From these data, then, he infers that sexual connection,

* Beweis, p. 40.

† Op. Citat. p. 444, *et seq.*

‡ See also Girdwood, Lancet, Dec. 1844, for facts of this nature.

to be fruitful, must take place within eight or twelve days from the cessation of the menstrual discharge.* Raciborski † thinks the time more limited. Out of sixteen women who gave him such information as enabled him to determine the time of fecundation, there was only one in whom this occurred so late as ten days after the cessation of the menstrual flux; and in this one the menses had been suddenly arrested several days before their usual time of cessation, so that the extrusion of the ovum, M. Raciborski thinks, did not take place till about two days prior to the act of sexual intercourse, to which it owed its fecundation. M. Raciborski relates several cases which seem to shew that impregnation may result from sexual coitus taking place one or two days before the period of menstruation. In one of these cases the menses did not appear at all; in three others they continued an unusually short time.

OF FECUNDATION.‡

UNTIL very recently, the opinion prevailed that in every case of impregnation, the seminal secretion made its way from the uterus along the Fallopian tubes to the ovary, where its fecundating influence was exerted on the ovum or ova, which were sufficiently mature to be acted upon; and by many it was also supposed, that unless the seminal fluid reached the ovary, no ova were extruded. Hence the statement of Professor Müller,§ that in Mammalia, impregnation is always effected at the ovary. Hence also the early remark of Bischoff, that in rabbits a period of from nine to ten hours, in bitches of from twenty to twenty-four hours, after the union of the sexes, elapses before any ova are extruded from the ovary. More recent experiments, made especially by Bischoff || himself, have proved, however, as already related, that the maturation and escape of ova from the ovary, is an event totally independent of the arrival of seminal fluid at the latter organ, and independent even of any union of the sexes. It is true that, as shewn especially by the experiments of Bischoff, sexual union in rabbits, bitches, and probably most other Mammalia, usually takes place previous to the extrusion of ova from the ovary (though this is denied by M. Pouchet ¶), and that sufficient time often elapses for the seminal fluid to reach the ovary before such extrusion occurs. And, doubtless, in these latter cases, fecundation of the ovum or ova is effected at the ovary itself. But the fact of ova having in several instances been

* Beweis, p. 44. More recently (Müller's Archiv. 1844. Jahresbericht, p. 132) Bischoff states as his conclusion from analogical reasoning and facts communicated to him, that the time of fruitfulness is limited to the twelve or fourteen days succeeding each menstrual period.

† Op. cit. p. 457, *et seq.*

‡ Müller's Physiology, p. 1488.

§ Physiology, p. 1491.

|| Beweis, &c. and Entwickelungs-geschichte des Hunde-eies.

¶ Theorie Positive de l'Evol. Spontan. &c. 1847, p. 372.

found considerably advanced along the Fallopian tube in animals killed immediately after or even before sexual union, not only proves the spontaneous maturation and discharge of ova from the ovary, but also renders highly probable the opinion, that not merely at the ovary, but at any part of the tract from this organ to the uterus at which the ovum first comes in contact with the seminal fluid, fecundation of it may be there effected. Bischoff* is of opinion that the ovum may sometimes be fecundated at the ovary, but that most commonly it escapes from this organ previous to the arrival at it of the seminal fluid, and that fecundation is then effected in the Fallopian tube. He considers that by the time the ovum reaches the uterus, or even the lower end of the Fallopian tube, its capacity for being impregnated is lost. His reasons for this supposition, are founded on the changes indicative of impregnation observed in the yolk of the ovum previous to its entrance into the uterus, and on the complete cessation of the sexual desire in those animals in which, after death, he found that the ova had passed into the uterus, or had arrived at the lower part of the Fallopian tube. Pouchet,† on the other hand, maintains that it is *only* in the uterus or the lowest part of the Fallopian tube, that fecundation takes place, for, according to his statement, the seminal fluid never penetrates so far as the ovary, and seldom, if ever, extends beyond the middle of the Fallopian tube. He believes that Bischoff and Wagner must have mistaken for spermatozoids on the ovary a form of Entozoa, which he describes under the name of Pseudo-zoospermes.‡

No confirmation has been afforded to the opinion entertained by Prevost, and Dumas, and by Dr. Barry,§ that the spermatozoids enter bodily into the ovum, and as believed by the first-named observers, constitute the embryo. Neither has any other embryologist succeeded in finding any opening or fissure in the zona pellucida, through which the spermatozoids might be enabled to enter the ovum, as was described by Dr. Barry: || Bischoff, who has repeatedly but fruitlessly made search for such an opening in the ova of bitches and rabbits, disbelieves entirely in its existence.¶

Fecundation in Plants.—In his enquiry into the question concerning the probable mode in which fecundation of the ovum of animals is effected, Professor Müller was led into an examination of the several theories adopted in explanation of the process of fecundation among plants; especially of those of Schleiden and Meyen. Since then, the opinion entertained by Schleiden that the extremity of the pollen-tube pushing the

* Entwickl. des Hunde-Eies, p. 30.

† De la Fécondation, p. 35, *et seq.*; de l'Evolution Spontan. p. 370.

‡ De l'Evol. Spont. p. 416.

§ Philosophical Transactions, 1840, p. 533; and 1843, p. 33. In the latter place Dr. Barry states that he has twice distinctly observed several spermatozoids within the zona pellucida of ova from the rabbit.

|| Müller's Physiology, p. 1497, and fig. 166 D.

¶ Entwickelungs-gesch. des Hunde-eies. p. 17.

embryo-sac before it becomes detached from the rest of the tube, and constitutes the first rudiment of the future plant, has been opposed by Professor Amici,* the celebrated Italian botanist, to whom we owe the discovery of the emission of tubes by the pollen grains. From observations made on the *Cucurbita Pepo*, Amici appears to have clearly ascertained that, although the extremity of the pollen-tube enters the nucleus of the ovule to a certain depth, yet, it never penetrates the embryonic sac; and he thinks it probable that the contents of the sac are fecundated by an absorption through its membranous wall of the impregnating fluid of the pollen-tube, which is situated in the immediate neighbourhood of the sac, or even on its external surface. As other reasons against the supposition that the extremity of the pollen-tube itself becomes the embryonic vesicle from which the embryo is formed, he observes, that this vesicle exists previous to the fecundation of the ovule, and that, after fecundation, its development commences at the opposite point to that at which the pollen-tube exercises its influence. Moreover, the true embryo of the plant may be distinctly recognised before it has acquired a diameter equal to that of the pollen-tube from which it has been supposed directly to spring. His investigations, likewise, into the mode of fecundation as pursued in the Orchidaceæ, have shewn him that in these plants also, the extremity of the pollen-tube is not converted into the embryo.

M. Tulasne†, on the other hand, from the examination of three species of *Veronica* and other plants, expresses himself as favourable to Schleiden's opinion. He states, that he has many times observed the pollen-tube to penetrate the embryo-sac, and this apparently by perforation. At no period has he been able to detect any thing which could be called an embryonic vesicle. He observes, that when the embryo-sac commences to enlarge, the plastic matter which it contains becomes developed into cells from the circumference towards the centre. During the early part of this cell-forming process, the pollen-tube within the embryo-sac remains apparently unaltered, and filled with grumous-looking material. Shortly, however, this material breaks up, and the tube which contains it becomes divided by a number of transverse septa into so many cells, which divide and subdivide: and then, in the midst of the resulting mass, the embryo appears. An opinion rather favourable to the penetration of the pollen-tube into the embryo-sac in the ovulum of *Avicennia*, has also been expressed by the late Mr. Griffith.‡

* An. des Sc. Nat. Avril, 1847. † Comptes Rendus, 14 Juin, 1847, p. 1060.

‡ Transactions of the Linnæan Society, vol. xx. 1846, p. 1—6.

RECENT ADVANCES

IN THE

PHYSIOLOGY OF DEVELOPMENT.

OF THE CHANGES IN THE OVUM PREVIOUS TO THE FORMATION OF THE EMBRYO.*

UNDER this head, it is proposed to bring together all the new facts relating to the subject, which have been derived from observations made on the invertebrate, as well as on the different classes of vertebrate, animals.

The most important subject for consideration, will be the division and subdivision of the yolk. Before entering upon this topic, however, it is necessary to inquire whether the ovum does not, immediately before, or immediately after, its extrusion from the ovary, undergo other changes previous to the manifestation of the remarkable phenomenon of spontaneous cleaving.

Changes in the germinal vesicle and germinal spot.—Dr. Barry stated, that, previous to the discharge of the ovarian ovum, the germinal spot returns to the centre of the germinal vesicle, and the germinal vesicle to the centre of the ovum; and that the germinal vesicle is not dissolved, but that while it and the germinal spot undergo the changes of place just mentioned, a peculiar process of cellular development occurs, which ends in the formation of two cells in the centre of the yolk, which have an important destination in reference to the formation of the embryo.† With reference to these various points, however, both M. Bischoff and Mr. Wharton Jones think that Dr. Barry's statements are erroneous. Bischoff describes the yolk of an ovarian ovum after coitus, as being unchanged in its characters, with the single exception of being fuller and more dense: it is still granular as before, and does not possess the layers of nucleated cells described by Barry. He thinks also, and in this opinion he is supported by Mr Wharton Jones, that the movement of the germinal vesicle and germinal spot from the surface to the centre of the ovum, could not possibly be observed even if they took place. Moreover, he is led by his observations to the conclusion that, contrary to Dr.

* Book the Eighth, section i. p. 1508 of Müller's Physiology.

† Third Series of Researches in Embryology in Philosoph. Transact. 1840.

Barry's opinion, the germinal vesicle does really cease to exist (as indeed, observers before Barry had generally supposed), very soon after coition.* But, at the same time, he thinks that it does not always disappear before the ovum leaves the ovary.† In many cases it cannot be discerned in the ovarian ovum several hours after the coitus; and mostly, not when the ovum has entered the Fallopian tube. But, in other cases, it is often discoverable many hours after coitus, both in the ovarian ovum and even in ova which have passed into the Fallopian tube. It is, however, invariably dissolved before the commencement of the other metamorphoses of the yolk, presently to be described.‡

It is worthy of remark, that in those intestinal worms of which the ova are very transparent, Kölliker § distinctly observed, that there was a period during which the germinal vesicle was no longer to be seen, although the development of cells, preparatory to the formation of the embryo, had not yet commenced. And, in these instances it appeared to him, that the germinal spot disappeared before the germinal vesicle.

Professor Wagner,|| on the other hand, seems to agree with Dr. Barry in respect of the fate of the germinal vesicle. For he says that, although, owing to the difficulty of the subject of investigation, he has not arrived at any absolutely conclusive result, yet he regards it as a certain fact, that within the germinal vesicle the germinal spot gives rise to new generations of cells which grow with great rapidity, and eventually cause the solution or destruction of the parent-cell, or germinal vesicle. He states, that he has distinctly witnessed this process of cell-formation by the germinal spot in the ova both of frogs and Mammalia.

The observations of M. Vogt on Alytes Obstetricans,¶ are rather in favour of the view entertained by Barry and Wagner. For he states, that when the ova of this batrachian approach maturity, the germinal spots increase in number, and that when the vesicle is burst by pressure, they escape in the form of transparent vesicles, which, in ova mature enough to leave the ovary, often amount to as many as forty. Moreover, he observed, that in ova which had been discharged from the female and fecundated only a few hours, the germinal vesicle, which before was visible even to the naked eye, could now by no means be discerned, and that the germinal spot also seemed to have disappeared, though, on farther search, several

* Entwickl. der Säugeth. und des Menschen, p. 42. † Ibid.

‡ The germinal spot, however, Bischoff supposed, from what he observed in the rabbit, not to be dissolved, like the germinal vesicle, but to be set free, and subsequently to undergo peculiar changes to which reference will again be made. Recently, however, Bischoff has had reason to doubt the correctness of the above view, for in two cases he could not detect any spot in the perfectly isolated germinal vesicle of bitches' ova. (Entwick. des Hunde-eies, p. 42.)

§ Müller's Archiv. 1843. p. 77.

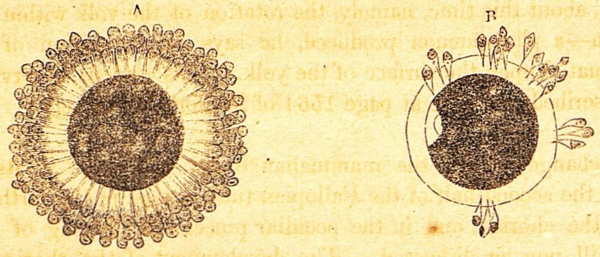
|| Lehrbuch der Physiologie, Second edit. p. 53.

¶ Untersuchungen über die Entwickelung der Geburtshelfer-Kröte. Solothurn, 1841. p. 4.

small clear vesicles, exactly similar to those mentioned as being formed within the germinal vesicle, were observed scattered through the yolk. It appears, therefore, that the fate of the germinal vesicle with its germinal spot, is still matter of uncertainty.

Changes in the tunica granulosa.—Both Barry and Bischoff have observed, that the cells of the membrana granulosa of the ovisac, which immediately surround and adhere to the ovum, undergo a peculiar change of form about the time at which the ovum is destined to leave the ovary. They become club-shaped, their pointed extremities being attached to the zona pellucida, so as to give the ovum a stellate appearance (see fig. 5). The club-

*Fig. 5.**



shaped extremity of each cell contains a distinct nucleus, and Barry states, that in place of this nucleus, a pellucid space is afterwards seen; that a young cell succeeds, and that subsequently, the whole cell becomes filled with other cells. Bischoff, however, has seen none of the latter appearances. But he has observed, that when the ovum enters the Fallopian tube, these cells lose their spindle-or club-like shape, and become quite round. In the bitch, they continue to invest the ovum in this round shape throughout the whole tract of the Fallopian tube—disappearing only when the ovum reaches the uterus †—but in the rabbit, they wholly disappear at its very commencement.

Contraction of the Yolk. Formation of the Chorion.—Besides the disappearance of the germinal vesicle, and, in the rabbit, the disappearance also of the cells of the membrana granulosa, it is observed, according to Bischoff, that in the upper part of the Fallopian tube, the yolk no longer completely fills the zona pellucida, but that a clear fluid collects between them, and that the contour of the yolk becomes defined by a dark line. This change Bischoff ascribes to a contracted and consequently more dense condition of the yolk, the granules composing which now adhere together so firmly, that when the yolk is broken down with a needle, they do not become diffused through the surrounding fluid, as they would have done previously.

* Fig. 5. A. An ovarian ovum from a bitch in heat, exhibiting the elongated form and stellate arrangement of the cells of the discus proligerus or membrana granulosa around the zona pellucida. B. The same ovum after the removal of most of the club-shaped cells.

† Entwickel. des Hunde-eies, p. 41.

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this and to its transparency, it is not easily recognised; but as the ovum reaches the lower part of the Fallopian tube, this new investment acquires considerable thickness, and shortly begins to assume the characters of the chorion, into which it, together with the zona pellucida, is subsequently converted.* At this part of its transit along the Fallopian tube, the ovum remains still unchanged in structure, and no alteration, beyond increased thickness, is perceived in the zona pellucida. A remarkable phenomenon has, however, been noticed by Bischoff, about this time, namely, the rotation of the yolk within the zona pellucida—a phenomenon produced, he says, by the action of vibratile cilia, situated upon the surface of the yolk. This curious observation has been described in a note at page 1564 of Müller's Physiology.†

The changes which the mammalian ovum undergoes in its passage through the second half of the Fallopian tube, consist in the further formation of the chorion, and in the peculiar process of cleaving of the yolk, which will now be discussed. The development of the chorion, will be considered at a future page.

Division and subdivision of the yolk.

This process has been long known to occur in the amphibia and fishes and some invertebrate animals. And observations of Dr. Barry, relative to the rabbits' ovum, seemed to shew that a similar change occurs in the ovum of mammiferous animals. This is now known with certainty to be the case. The exact nature of the process is, however, still involved in doubt, and very different opinions respecting it are entertained by different physiologists.

The phenomena are observed with more difficulty in the higher than in the lower animals. Hence, it seems desirable to detail those which have been recently investigated under favourable circumstances, and with great ability, by Professor Kölliker ‡ and Dr. H. Bagge,§ in many of the In-

* This deposit of albuminous matter around the ovum, first described by Mr. Wharton Jones, appears to have been yet observed only in the rabbit; no such deposit takes place around the ovum of the bitch (Bischoff, l. c. page 46), in which animal the chorion is formed from the zona pellucida alone.

† The rabbit appears to be the only mammalian animal in whose ova this rotation of the entire mass of the yolk, previous to cleavage, has been observed. Bischoff has never detected it in the bitch's ovum, but the Fallopian tube in these animals is so thick and opaque, that the phenomenon might occur without being perceived (Entw. des Hunde-eies, p. 46).

‡ Entwickelungs-geschichte wirbellöser Thiere, Müller's Archiv. 1843, p. 68; and Entwickl. der Cephalopoden, Zurich, 1844.

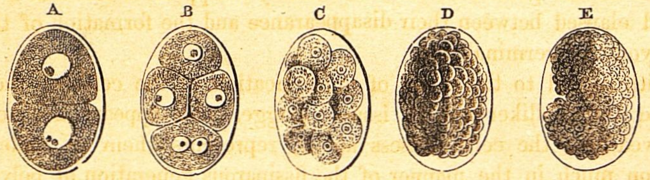
§ De Evolut. Strongyli auric. et Ascarid. acum. Vivip. Diss. Inaug. Erlangæ, 1841.

vertebrata, before noticing the corresponding changes which have been observed to take place in the ova of Mammalia.

In the Invertebrata.—From the investigations of the former of these observers, it would appear, that the early structural changes undergone by the substance of the impregnated ovum, are of several varieties in the different invertebrate animals; but that, so far as has yet been ascertained, these varieties are referable to three principal types. In the first type, the whole substance of the yolk undergoes the process of division and subdivision. In the second, the process is confined to a portion of the yolk. And, in the third type, the yolk does not take any part in the process, but certain transparent nucleated cells, arising in its interior, undergo multiplication in the same manner as the yolk itself in the former varieties: the substance of the yolk in this third type being gradually absorbed during the process.

I. The first of these types is exemplified in the ova of three species of Ascarides, namely, Ascaris nigrovenosa, A. acuminata, and A. succisa.* Kölliker † states, that as soon as the mature ova of one of these worms reach the fundus of the uterus, the first signs of impregnation are manifested by the disappearance of the germinal vesicle, and a diminution in the consistence of the yolk, the granules of which adhere together less firmly than before. Shortly after this change, a new nucleated cell appears in the centre of the yolk, which then again acquires a closer texture, a smaller circumference, and a more definite outline. After a time, two cells instead of one are perceived in the interior of the yolk, and soon the yolk

Fig. 6. ‡



itself divides into two halves, each of which contains one of the cells in its centre (fig. 6, A). Then, again, each of the two cells is replaced by two others, and the substance of the yolk becomes divided into four

* The development of these Entozoa was described by Von Siebold (Burdach's Physiologie. Second edition, vol. ii.), but has been more recently and more accurately investigated by Bagge and Kölliker in the essays above alluded to.

† Müller's Archiv. 1843, p. 103.

‡ Fig. 6. Cleaving of the yolk after fecundation. A. An ovum, the yolk of which is divided into two equal portions; the upper portion contains a cell with a large nucleus, the lower, a similar cell with two small nuclei. B. An ovum, of which the yolk is divided into four masses, three of which possess a single nucleated cell, the fourth, two such cells. C. An ovum, the globular masses of whose yolk amount to sixteen, in each of which a

masses, corresponding to the four cells which they enclose within them (B). This process of division, by which each cell, and consequently each mass of yolk-substance, is resolved into two others of half the size of the original, is repeated until the yolk is converted into an oval mass composed of globules, in the interior of each of which, the existence of a nucleated cell can be distinctly discerned (C). Beyond this point, however, the cells can no longer be recognised, though the process of division continues, and the globular masses become smaller and smaller (D, E), until, eventually, they begin to be moulded into the form of the young worm, in the construction of which they all take part.

Such is a general outline of the process as it occurs among these varieties of Ascarides, and has been observed also among several other invertebrate animals. There are certain questions, however, which present themselves for solution in the further consideration of it. These are—

What is the mode of origin of the first cell seen within the yolk after the disappearance of the germinal vesicle ?

What is the mode of multiplication of this cell ?

How is the division of the yolk produced ?

Are the different segments of the yolk to be regarded as cells ?

Neither Bagge nor Kölliker observed any facts which afford an answer to the first question. For they were unable to perceive the first embryonic cell within the yolk until it was completely formed. This much, however, seems certain, that the cell is not developed from the germinal spot or nucleus of the germinal vesicle. For in the perfectly transparent ova of Ascaris dentata, Kölliker satisfied himself that the germinal spot as well as the germinal vesicle invariably disappeared, and that a certain period elapsed between their disappearance and the formation of the first embryonic or germinal cell.

With regard to the mode of multiplication of the cells of the yolk, Bagge and Kölliker are at issue. Bagge, who appears not to have observed that the cells possess nuclei, represents them as undergoing division much in the manner of the fissiparous generation of polygastric animalcules. But Kölliker has shewn that each cell is nucleated, and that sometimes one large cell contains two small nuclei in place of one of twice the size. And as he has observed in other Entozoa that the same cells multiply by the development of two young cells from the two halves of the divided nucleus within the parent cell, which then disappears, he draws the fair inference that the same process occurs in these Ascarides also. A similar opinion is entertained also by Dr. Sharpey.*

It would seem that the division of the yolk is a consequence of the

nucleated cell is clearly discernible. From Ascaris nigrovenosa. (After Kölliker.) D. and E. are representations of ova from Ascaris acuminata, shewing subsequent steps in the process of division described in the text. (After Bagge, op. cit.)

* Quain's Anatomy. Fifth edition, p. l.

multiplication of the cells. For, it is not until two cells have appeared in place of the one which previously occupied the mass of the yolk, that the latter begins to undergo division. Kölliker therefore regards the division and subdivision of the yolk, as the consequence of an attractive force exerted by the germ-cells on the vitelline or yolk-substance.* And Dr. Sharpey † remarks, that the shrinking of the granular mass of the yolk around the first central cell, is in harmony with this view. Dr. Sharpey also mentions the fact, that on one occasion while he was examining the ova of one of these Ascarides, at the time when one of the large segments into which the yolk is first cleft, divided itself into two portions, he observed a very obvious heaving motion among the granules throughout the whole mass; then ensued a constriction at the circumference, which, proceeding inwards, soon completed the division.‡

Kölliker thinks that the earlier divisions of the yolk cannot be regarded as cells, for they appear to him not to be enveloped with a membrane. Dr. Sharpey,§ on the other hand, is disposed from his observations on the ova of Ascaris, to admit the existence of an enveloping membrane, and consequently he regards these larger, as well as the later and smaller subdivisions of the yolk, as complex cells, analogous in their structure to the unimpregnated ovum, and to the nucleated globules of the nervous system.||

* L. c. p. 108. † Loc. cit.

‡ In relation to this question concerning the cause of the division of the yolk, may be also mentioned the results of some observations recently made by Vogt on the development of the Molluscous Gasteropods. (Ann. des Sci. Nat. 1846. Zoologie, p. 23, *et seq.*) According to this embryologist, the yolk of the ovum of Acteon viridis (on which his observations were almost exclusively made) consists, immediately after impregnation, of a gelatinous substance containing numerous minute granules, and having in its centre a round transparent vesicle appearing as a clear space. Shortly afterwards the vitellary mass divides into two equal portions, in the centre of each of which is contained a clear vesicle, like that before observed in the centre of the yolk itself. But, contrary to the above-stated opinion of Kölliker, and to that of most other embryologists, Vogt believes that, at least in Acteon, the division of the vitellary mass, instead of being a consequence of the multiplication of the central vesicle, precedes, and is the cause of, the latter phenomenon. The only evidence, however, on which this opinion appears to be based is, that in one instance Vogt observed an ovum in which one of the two portions into which the yolk was dividing was somewhat smaller than the other, as if of more recent formation, and did not contain a vesicle.

§ Quain's Anatomy, p. 1.

|| According to Vogt's observations, the very earliest divisions of the yolk-mass, in the ovum of Acteon, are unprovided with an enveloping membrane, yet, by the time the number of segments has amounted to twenty-four, evidences of an investing membrane around each may usually be observed. (Further observations on this subject will be made when considering the process of division and subdivision of the yolk as it occurs in the mammiferous ovum.) A remarkable peculiarity has also been observed by Vogt in the products of the division of the yolk in this animal. The first two divisions of the vitellary mass subdivide as in the ova of other animals, and produce four equal-sized spheres, arranged together in a crucial form, and each possessed of a central transparent vesicle. But in the

II. In the second variety of the process of yolk-cleaving, only a part of the yolk is the seat of this phenomenon. The only invertebrate animals in which this variety has been observed, are the Cephalopods, and a description of the process as it occurs in the ova of these animals has been furnished by Kölliker from observations on the Sepia.* In the unimpregnated ovum of this animal, as in those of fishes, and Alytes obstetricans,† the germinal vesicle is situated at one part of the surface of the yolk, instead of being imbedded in the centre, as it is in most other cases. And the process of cleaving commences in the situation of this vesicle, and in the Sepia, is confined to its immediate neighbourhood. Shortly after the disappearance of the germinal vesicle, consequent on fecundation, a slight elevation of the yolk appears at that part of the surface where the vesicle was situated. This elevation soon divides into two prominences, within each of which is contained a nucleated cell, surrounded by granular matter. The two prominences are shortly divided into four, and then into eight, segments, each containing a cell surrounded by granules. These segments have the form of segments of a circular disc, all meeting with round, well-defined, prominent ends at the centre, where the nucleated or embryonic cells are situated; but at the periphery of the circle, passing, without any definite line of separation, into the yolk. At the next stage the eight segments of the circle give off at their apices eight globular segments, which form a ring within the radiating segments. Each globular segment, as well as each newly-formed apex of the radiating segments, contains an embryonic cell. All these segments then divide, so that there result sixteen radiating, and sixteen globular segments, in each of which is an embryonic cell. A new

next stage of the process, the four spherical masses, instead of dividing into eight smaller equal-sized spheres, retain, as nearly as possible, their original size, while from one surface of the crucial-shaped plane which they form, four other spherical bodies gradually arise, which, when fully formed, are about half the size of the large ones, and much more transparent, owing to the very few granules which they contain; each possesses a clear vesicle similar to that in the larger spheres. It did not appear as if these smaller masses were formed by a division of the larger spheres, for, as above stated, these latter maintained almost their original size; they seemed rather to be produced by a kind of exudation from the large masses of the more viscous part of the yolk-substance, few granules entering into their composition. After this event, the several segments of the yolk go on dividing and subdividing in the ordinary way, and the difference in size between the two above-mentioned sets of spheres shortly disappears; but throughout the whole process the divisions of the larger set remain granular and opake, while those of the small set continue to be characterized by their transparency. When the process of cleaving is complete, the former are all found in the centre of the yolk, and are accordingly named by Vogt the central spheres, while the latter are situated at the surface, and are hence termed by him peripheral spheres. From the central opake spheres, or cells as they have by this time become, he states that the central parts of the embryo are formed while the peripheral organs are developed out of the transparent spheres or cells.

* Entwickelungs. der Cephalopoden, pp. 17—40.

† Entwickel. der Geburtshelferkröte, p. 1.

ring of globules with cells is then formed, whereupon these and the radiating segments again suffer division in the direction of the radius of a circle. This process is repeated; the radiating segments meanwhile extending at the periphery, while they are shortened and narrowed at their apices by the divisions they undergo. At length these divisions reach a stage, when the apex of each radiating segment is given off together with the embryonic cell, leaving no remaining cell in the apices. When this takes place, the radiating segments disappear, or cease to be distinguishable from the rest of the yolk. Henceforward the germinal space contains only globular segments of yolk, each including an embryonic cell; the globules being smallest in the centre. Kölliker maintains that neither the earlier divisions of the yolk, nor even the last small globules, can be regarded as cells. For the segments and the first formed, larger, globules are, he says, merely hillocks of elementary granules on the surface of the yolk collected around the embryonic cells. And the small globules appear to differ from these only in their size, and in containing more granular matter. In the Sepia, as in the Ascarides, Kölliker is of opinion that the division of the yolk into segments or globules, is dependent on some attractive force, exerted by the nucleated embryonic cells upon the substance composing the yolk, and that the cells themselves multiply, as in the Ascarides, by the development of two young cells within each parent-cell.

III. The third variety of the changes which take place in the yolk in invertebrate animals, subsequently to fecundation and the disappearance of the germinal vesicle, is exemplified in the ovum of Ascaris dentata; and the observations which Kölliker* has made on the changes of the yolk in this Entozoon are of great importance, since, owing to the almost complete transparency of the ova and their coats, it is scarcely possible that any error of observation can have been committed. In these investigations Kölliker found that, for a short time after the disappearance of the germinal vesicle, the ovum is seen to contain merely the transparent fluid of the yolk, with very scanty elementary granules. But soon the first embryonic cell is developed in the centre of the yolk. This cell is quite transparent, globular, somewhat larger than the previous germinal vesicle, and has a small, pale, round nucleus attached to its wall. As the ova advance through the cavity of the uterus, this embryonic cell is replaced by two similar cells; then four such cells are seen, then eight, and so on, the cells becoming more and more numerous, and diminishing in size as they increase in number. While these cells are thus undergoing multiplication in the centre of the yolk, the yolk itself suffers no change except in quantity; it gradually disappears, being consumed, as it would seem, in the growth of the embryonic cells. These, while they multiply, occupy more and more space, for although each of

* Müller's Archiv. 1843, pp. 76—85.

the two new cells is smaller than the one which preceded them, yet the two together occupy much more space than it did. So that at length the yolk-membrane or ovum is completely filled with a mass of small cells, in which the nucleus can no longer be distinguished; and at a still later stage even their cell-like form cannot be distinguished, and the mass, which now begins to take the form of the young worm, seems to be composed merely of granules.

In this Entozoon Kölliker has distinctly observed, that the mode of multiplication of the cells consists in the development of two young cells within each of the cells of the preceding generation; the parent cell then undergoing solution aud disappearing. Kölliker believes that the development of the two new cells is dependent on the previous division of the nucleus of the parent-cell, each division of the nucleus giving rise to a new cell. For in the ova of Cucullanus elegans, in which the process just described from Ascaris dentata is repeated, he has often observed cells the nuclei of which were, in some instances, elongated, in others, constricted in the middle, while in other cells there were two nuclei in place of one, these two being smaller than the single nucleus of the neighbouring cells, and situated, in some cases, close together, in others, more removed from each other (fig. 7). His opinion is made more probable also, by the fact of his having seen in ova of Ascaris dentata, two small nucleated cells enclosed within a parent-cell which had no nucleus (see fig. 8, C).

Fig. 7.*

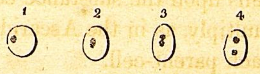
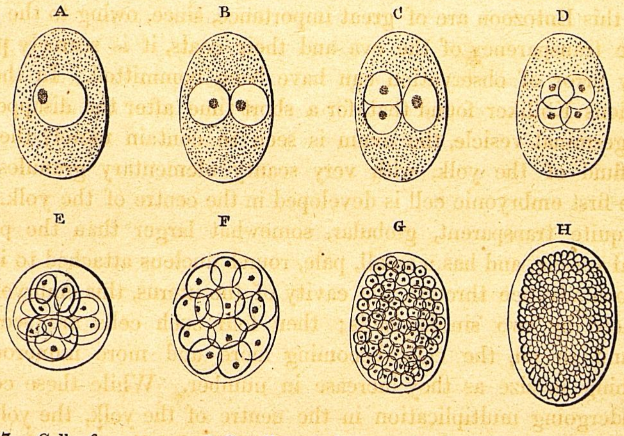


Fig. 8. †



* Fig. 7. Cells from ovum of Cucullanus elegans, shewing supposed division of the nucleus in the manner just described. (After Kölliker.)

† Fig. 8. A, B, C, D, successive stages of the ovum of Ascaris dentata, shewing duplication of cells. E, F, G, H, ovum of Cucullanus elegans, shewing the advance of the process. (After Kölliker.)

From the preceding account of the three principal varieties of the process which intervenes between the disappearance of the germinal vesicle and the formation of the embryo, in Entozoa and many other invertebrate animals, it will be apparent, as Kölliker remarks, that the more essential part of the process is the development and multiplication of nucleated embryonic cells, which become smaller as they increase in number, and at length form the granular mass out of which the embryo is moulded. The part played by the yolk appears to be a subordinate one: the peculiar process of division and subdivision, which, in some cases, it undergoes—whether this affects its whole mass, or only a limited portion of it—being determined and regulated by the development and increase of the embryonic cells.

In Amphibia and Fishes.—It remains to inquire how far the phenomena observed in the ova of vertebrate animals agree with those which we have just been considering: and, first of all, to apply the facts with which we have become acquainted, to the explanation of the analogous process in Amphibia and Fishes.

That variety in the process which consists in the whole yolk undergoing division and subdivision, was discovered long since, in the ova of frogs, by Prévost and Dumas,* and afterwards described with great accuracy by Von Baer.† Baer, however, seems to have entertained no suspicion that the segments of the yolk are other than solid homogeneous masses of the yolk-substance. Rusconi,‡ in criticizing Baer's account of the process, remarked, that there were cavities in each of the eight masses into which the dark half of the yolk divided, and was probably led to make this remark by seeing the transparent embryonic cells. But Bergmann § first announced that each of the masses of the yolk contained a transparent body, which he supposed to be a solid nucleus.

From these observations, though imperfect, the most natural inference is, that the process described by Bagge and Kölliker, as taking place in the ova of Strongylus auricularis, and Ascaris nigrovenosa, and acuminata, takes place also in the frog, and that the division and subdivision of the yolk is dependent, in the latter animal, as in those Entozoa, on the development and multiplication of embryonic cells. Kölliker|| indeed states, that he has seen nuclei in the vesicles which occupy the centre of the segments of the yolk in the frog's ovum. The earlier statements of Reichert,¶ too, respecting the structure of the yolk at the end of the process of cleaving are also reconcilable with that view. The smaller corpuscules, he describes, may be the last generation of the embryonic cells, still surrounded by

* Müller's Physiology, p. 1508. † Ibid. p. 1509, and fig. 168.

‡ Müller's Archiv. 1836, p, 218.

§ Müller's Physiology, p. 1509 note; and Müller's Archiv. 1841, p. 89.

|| Entwickelungs-geschichte der Cephalopoden, p. 121.

¶ Müller's Physiology, p. 1512.

some of the yolk-substance. The larger corpuscules may, in some cases, be segments containing each an embryonic cell.*

It must be mentioned, however, that Bischoff has never been able to detect any nuclei in the transparent corpuscules or vesicles contained in the segments of the yolk of the frog's ovum, and, therefore, does not regard them as true cells. In other of the Amphibia, as Alytes obstetricans, and also in fishes, the process of cleaving affects only a part of the yolk, as in the second type described in the invertebrate animals. The external characters of the process as witnessed by Rusconi in the tench (Cyprinus tinca), are described at page 1510, of Müller's Physiology. The more intimate nature of the changes have been investigated by Vogt, in Alytes† and Coregonus palæa‡ (one of the salmon tribe). In Alytes, the cleaving affects only one half of the ovum, and, according to Vogt, only the surface of the yolk. For, at that stage of the process, when the surface is mulberry-like, the different segments, though rounded and defined towards the exterior, are towards the interior uninterruptedly continuous with the general substance of the yolk, just as is the case with the earlier segments of the ovum of Sepia. The segments contain (for the most part), each, a transparent round vesicle; and after the process is completed, and previous to the appearance of the embryo, the whole yolk is composed of cells, in the centre of each of which, a similar transparent vesicle, as a nucleus, is

* Reichert's later account (Müller's Archiv. 1841, p. 523) of the process of cleaving in the frog's ovum does not accord with the facts observed by other anatomists. The opinion which he advances is, that the smaller corpuscules which he finds composing the ovum at the end of the process, and regards as cells, all exist completely formed before impregnation takes place. Not, however, that he regards these cells as existing in a free state, but every two or three included within larger cells, and these again in still larger, and so on: the cells of each set enclosing within them smaller cells, and being themselves enclosed within larger, and all being contained within two large cells, which, in their turn, are held together by an investing membrane forming one large cell. The process of cleaving thus consists, according to Reichert, simply in the liberation, first of the two large cells, and then of each successive set of enclosed cells, by the solution of the including cells, till at length the smallest nucleated cells, destined to form the embryonic structures, are set at liberty. The facts really observed on which this hypothesis is based, seem to have been very few and very inconclusive. In a still more recent account (Muller's Archiv. 1846, p. 196), of the process of cleaving in the ovum of Strongylus Auricularis, Reichert modifies this opinion, and admits that the process really consists in the formation of successive crops of new cells. Even the largest segments of the ovum, he (like Dr. Sharpey) regards as true cells, and he states that in the process of duplication the nucleus of each such cell first breaks up into a number of oil-like particles which mix with the granular contents of the cell, that then this mixed mass gradually divides into two equal portions, each of which becomes invested with a distinct membrane; and that, subsequently, a clear vesicular body or nucleus forms in the centre of each. When fully formed these two cells are liberated by the solution of the parent cell-wall, and then undergo a similar process of division; the nucleus of each invariably disappearing before the division commences.

† Entwickelungs-gesch. der Geburtshelferkröte.

‡ Histoire Natur. des Poissons d'eau douce, by M. Agassiz. Tome i. 1842.

situated: the contents of each cell consisting of the granules and lamellæ of stearine, which previously constituted the yolk. These facts accord with the observations of Kölliker, on the sepia and intestinal worms. But other parts of Vogt's description cannot be reconciled with Kölliker's views: for instance, the statements that the cleaving of the yolk is produced by folding in of the yolk membrane: that some of the segments have no cell-nucleus, while others contain several: and that the formation of the cells last described, is not coincident with the cleaving, but begins after the cleaving-process has wholly ceased—a space of time intervening in which nothing like cells exist. Vogt believes, too, that the transparent cells which are contained in the segments of the yolk, are multiple germinal spots, which remain when the germinal vesicle, in consequence of impregnation, disappears, and which exist in the yolk before the process of cleaving commences (see page 63). Between Vogt's account of the process in Coregonus, and Kölliker's description of the division and subdivision of the yolk in Sepia and other Invertebrata, there is much apparent discrepancy. Kölliker, however, thinks that they may be reconciled. As there is, however, much that is indefinite in Vogt's description, further consideration of it need not be entered into here. It may be remarked, however, that Vogt is of opinion, that here also the germinal spots play an important part in bringing about the changes in the yolk, which precede the formation of the embryo.

In Birds, nothing like a cleaving of the yolk has hitherto been observed. It is supposed that the extent of the yolk implicated in the process may be very limited. It may be, perhaps, that the process does not affect the yolk itself, but consists solely in the development and multiplication of embryonic cells, in the central cavity of the yolk, such as is described by Kölliker in Ascaris dentata and Cucullanus elegans (see page 71, and fig. 8), but without the simultaneous absorption of yolk substance, such as takes place in those Entozoa.*

In Mammalia.—Lastly, the nature of the process which takes place in the ova of Mammalia must be inquired into.

The changes which the yolk of the rabbit's ovum undergoes, during its transit through the Fallopian tube, have been investigated by Dr. Barry and Professor Bischoff:† and, more recently, the analogous changes which occur in the bitch's ovum have also been examined by Bischoff.‡ Dr. Barry's earlier observations were given at page 1565 of Müller's Physiology. His later Researches § afford results, which in respect to the more im-

* M. Coste (Comptes Rendus, 5 Avril, 1847,) states, however, that he has observed the process of cleaving in the ovum of birds during its passage along the oviduct; and he remarks that it is limited to that portion of the yolk which constitutes the cicatricula.

† Entwickelungs-geschichte des Kaninchen-eies, 1842.

‡ Entwickelungs-geschichte des Hunde-eies, 1845.

§ Third Series, Philosophical Transactions, 1840.

portant and trustworthy points, are confirmatory of these earlier ones. And if merely the figures which he gives be examined (see the figures copied in Müller's Physiology, page 1567, and the plates in Dr. Barry's second and third Series of Researches on Embryology),* it will be seen that the appearances in the rabbits' ova taken from the Fallopian tube, agree in the most important points with the account of the first type of the process of cleaving observed by Bagge and Kölliker, in the ova of the three varieties of Ascaris. For Dr. Barry not only saw the division and subdivision of the yolk, but he also distinguished a pellucid space or nucleus in each of the segments, and he seems to have observed the development of two embryonic cells within the first single cell which takes the place of the germinal vesicle in the yolk, the subsequent development of two younger cells within each of these, and the continued repetition of this mode of multiplication.

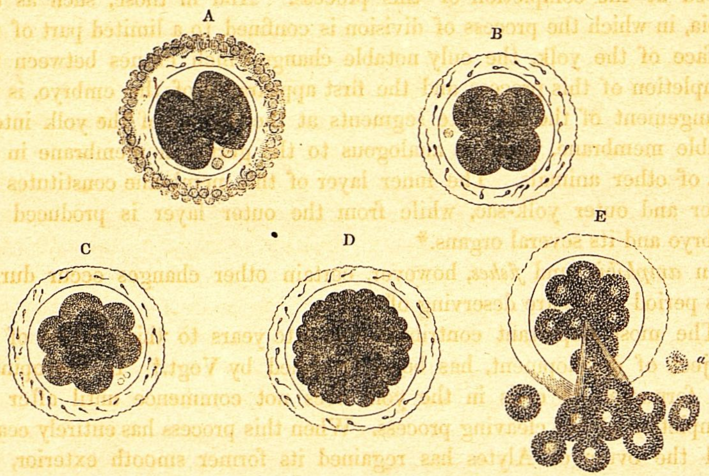
The description of the process given by Bischoff, as he witnessed it in the ova of the rabbit and of the bitch, is generally similar to Bagge's account of what he observed in the Strongylus auricularis. When, in these Mammalia, the ovum has passed the middle of the Fallopian tube in its transit to the uterus, the yolk, which was previously one compact uniform mass, begins to be resolved into a number of smaller spheroidal masses; first into two, then into four, then eight, then sixteen, and so on (see fig. 9). Each segment contains a transparent vesicle, which is seen with difficulty, especially in the bitch's ovum, on account of its being enveloped by the yolk granules, which adhere closely to its surface. This vesicle, Bischoff says, when liberated from the surrounding yolk granules, most nearly resembles a fat or oil-globule. He has never been able to detect a nucleus in it, though he has repeatedly and carefully examined it for this purpose in the ova of the rabbit and the bitch. Bischoff, therefore, cannot subscribe to the opinion, that the central vesicle of each globular segment of the yolk is a nucleated, or embryonic, cell. Neither does he regard the globular segments themselves as cells, for he states that neither in the rabbit nor in the bitch can any investing membrane be discerned. He considers them as simple aggregrations of yolk substance around the central body or vesicle, such as the earlier divisions of the ova of Ascarides nigrovenosa and acuminata and those of Sepia are, according to Kölliker.

It will be seen that the mode of division and subdivision of the yolk of the mammal's ovum, agrees in its principal and more obvious features with the first type described at page 66, as occurring in invertebrate animals. The process cannot, however, be regarded as essentially the same in the two cases, until the central vesicles of the segments in the mammal's ovum shall be shewn to be nucleated cells, the nuclei of which multiply by division, and thus determine the multiplication of the cells, two new

* Philosophical Transactions, 1839 and 1840.

cells being produced within each parent-cell. But no observer has yet seen a nucleus in any of the central vesicles of the yolk segments of the ovum of Mammalia. Bischoff remarks, however, that these vesicles,

Fig. 9.*



though not nucleated, evidently play the part of nuclei in the spherical yolk segments, and that the aggregation of the yolk substance into spherical segments must be due to a kind of attraction exerted by the vesicles. How the multiplication of the vesicles takes place, by which the subdivision of the yolk is effected, he cannot decide. But he sees no positive objection to the belief that they themselves multiply by division.†

Changes in the ovum subsequent to the process of cleaving.

With respect to the changes which occur in the ova of *invertebrate animals* after the completion of the process of cleaving, or analogous processes, little need be added to what has been already said. For

* Fig. 9, A. Ovum of a bitch, from the Fallopian tube, half an inch from its opening into the uterus, shewing the zona pellucida with adherent spermatozoids, the yolk divided into its first two segments, and two small granules or vesicles contained with the yolk in the cavity of the zona. B. Ovum of a bitch from the lower extremity of the Fallopian tube: the cells of the tunica granulosa have disappeared: the yolk is divided into four segments. C. Ovum of bitch from the lower extremity of the Fallopian tube, in a later stage of the division of the yolk. D. An ovum from the uterus: it is larger, the zona thicker, and the segments of the yolk are very numerous. E. Ovum from the lower extremity of the Fallopian tube burst by compression: the segments of the yolk have partly escaped, and in each of them a bright spot or vesicle is visible.

† Bischoff, Entwickelungs-geschichte des Hunde-eies, pp. 45, 46.

in those invertebrate animals, such as certain Ascarides and other Entozoa, in which the whole yolk is included in the cleaving or other process which ensues shortly after fecundation, the embryo is at once formed out of the entire mass of particles into which the yolk is resolved at the completion of this process. And in those, such as the Sepia, in which the process of division is confined to a limited part of the surface of the yolk, the only notable change which ensues between the completion of this process and the first appearance of the embryo, is the arrangement of the ultimate segments at the surface of the yolk into a double membrane, which is analogous to the germinal membrane in the ova of other animals. The inner layer of this membrane constitutes the inner and outer yolk-sac, while from the outer layer is produced the embryo and its several organs.*

In *amphibia* and *fishes*, however, certain other changes occur during this period which are deserving of notice.

The most important contribution of late years to this portion of the subject of development, has been furnished by Vogt.† In his opinion, the formation of cells in the yolk does not commence until after the completion of the cleaving process. When this process has entirely ceased and the ovum of Alytes has regained its former smooth exterior, the central part or yolk-nucleus (Dotterkern) is observed to have a darkish yellow colour, while the external cortical part, which is composed of molecular corpuscules, among which are scattered a few free germinal cells or vesicles (see page 63), has a whitish aspect. After a period of apparent rest ‡ succeeding the completion of the cleaving process of the yolk, the development of cells commences at that part of the cortical portion of the ovum at which the embryo subsequently appears, whence it extends over the remaining surface of the yolk and towards the interior. This formation of cells, according to Vogt's account, takes place by the production of an enveloping membrane around each of the germinal cells or vesicles already existing in the cortical substance. A portion of the granular material of the ovum is included between each germinal cell and the newly-formed investing cell-membrane, and constitutes the nutritive contents of the yolk-cell. It would seem, also, that new germinal cells are being continually formed, and then, by the above process, developed into yolk-cells. The first set of yolk-cells which are produced, accumulate at the surface of the ovum, and adhere together so as to form a membranous layer, which gradually extends over the entire surface, and increases in thickness as fresh quantities of cells are deposited on its interior.

Within the substance of this membrane is subsequently developed the earliest trace of the embryo, namely, the primitive groove, bounded by

* Kölliker, Entwickelungs-geschichte der Cephalopoden, p. 61.

† Entwickelungs-geschichte des Geburtshelferkröte, and Histoire Naturelle des Poissons, par M. Agassiz, t. i.

‡ Entwick. des Geburtshelferkröte, p. 10.

the two lateral masses, the laminæ dorsales. After the formation of yolk-cells has proceeded to a certain extent in the cortical part of the ovum, a similar process commences in the central portion. In this part of the ovum, however, there are originally no germinal cells; and it would seem, according to Vogt,* that at this period clear transparent cells, exactly similar to the germinal cells, are developed here; and that then an investing membrane forms around each of them, and thus produces so many yolk-cells in the same manner as those of the cortical part are formed. The cells of the central part of the ovum differ, however, from the cortical ones, in being larger, of an irregular form, and possessing stearine, instead of granular matter, as their contents. During the early period of the cell-formation in the central part of the ovum, gradual transitions in form and other characters, from the cortical to the central cells, may be perceived as the ovum is examined from without inwards. But at a later period the cortical cells become more and more distinctly separated from the central ones, and eventually constitute a perfectly distinct layer, which can be completely separated from the central portion of the ovum, without injury to either. On comparing the description furnished by Reichert† of the composition of the frog's ovum subsequent to impregnation, with Vogt's account as given above, it will be observed that, at least with regard to the variety in size of the cells of the yolk, a close similarity exists between them. But concerning the nature of these two kinds of cells or corpuscules, the changes which subsequently ensue in them, and the relative share possessed by each in the formation of the embryo, considerable discrepancy is observed in their opinions. By Reichert it was assumed that the large central cells, which at first are unprovided with nuclei, subsequently became nucleated, that young cells are then developed within them, and that, in proportion as they approach the periphery of the yolk so do the young corpuscules within increase in size; and eventually the membranous wall of the parent-cell disappears, while the small liberated cells constitute the formative mass out of which the several parts of the embryo are developed. And this, he considers, goes on until the whole of the large yolk-cells are resolved into broods of smaller cells; and the nearer these larger cells are to the centre of the yolk, the later are they in the production of young cells in their interior. The whole of this view, however, is contradicted by Vogt,‡ who observes that, at least in the ovum of the toad, no trace of young cells contained within parent-cells can be detected at the centre or any other part of the substance of the yolk; and he considers that the young cell which Reichert figures within a larger one§ is simply the germinal cell, around which the larger yolk-cell has formed, in the manner already described. In Vogt's opinion, as already expressed, the peripheral

* Entwick. des Geburtshelferkröte, p. 11. † Müller's Physiology, p. 1512.

‡ Entwick. des Geburtshelferkröte, pp. 34—40.

§ See fig. 170, p. 1513, Müller's Physiology.

cells of the yolk are developed as primary and independent structures, just as the central cells are; and the only probable way in which the latter may contribute to the production of subsequent sets of the peripheral cells, is by providing the nutritive material, or intercellular substance, out of which fresh quantities of new cells may be formed to supply the place of those consumed in the successive development of the several parts of the embryo. In the ovum of the young salmon, also, there is complete absence of anything like the production of young cells within larger ones. Indeed the yolk of the salmon's ovum appears to consist almost entirely of a clear gelatinous homogeneous fluid, without cells or corpuscules of any kind; the only trace of cells being found at the periphery in the immediate neighbourhood of the developing embryo.*

The difference in the opinions, therefore, of these observers, concerning the nature and ultimate condition of the two sets of cells found in the yolk soon after the completion of the cleaving process, appears to consist essentially in this: that, whereas, Reichert regards the smaller peripheral cells as the offspring of the large central ones, and is of opinion that all the larger cells are eventually resolved into broods of similar small ones, from which the embryo and its several parts are formed, Vogt believes that the peripheral and central cells are essentially different from each other, and are each destined to perform a separate part in the development of the embryo. The earliest formed cells of the periphery of the yolk, in the opinion of the latter observer, are employed to lay down the foundations of the embryo and of its principal organs, and in the immediate neighbourhood of each of these cells (but not within them), successive broods of new cells are subsequently developed to supply the wants of the growing parts: while the cells of the centre of the yolk, on the other hand, appear to have no other purpose than to elaborate fresh nutritive material or cytoblastema, out of which the above mentioned successive growth of new cells may be effected. As each of these large cells discharges its nutritive contents, it dissolves and disappears: being directly concerned neither in the formation of any part of the embryo, nor in the production of fresh broods of cells, and differing, therefore, in both these respects, from the cells of the peripheral part of the yolk. Another important point of difference in the opinions of Vogt and Reichert, as may be deduced from what has just been said, is that the latter considers the whole of the yolk to be directly concerned in the formation of the embryo and its several parts: while Vogt refers this formation entirely to the peripheral or cortical portion. In this view, Vogt is supported by several facts, especially by what he has observed in the development of the embryonic salmon; for, in the ova of these animals, the yolk, as before remarked, consists almost entirely of a homogeneous fluid substance in which there is no appearance of cells, except at the very surface, where alone the embryo is formed: the remainder

* Hist. Nat. des Poissons, t. i. p. 11.

of the yolk must, in this case, therefore, be regarded merely as a nutritive fluid.

According to Reichert's account of the development of the embryo frog,* it would seem that the first act of the process consists in the formation at the surface of the ovum of a fine membranous layer of cells, which, by extending over the whole surface, shortly constitutes a complete investment surrounding the yolk. And, in his opinion, it is not until this investing membrane is completely formed, that the development of the first formed parts of the embryo — namely, the two oval masses and the primitive groove between them—commences. From the observations of Vogt,† however, it appears that, in the development of the toad, no such investing membrane is formed. The earliest peripheral yolk-cells, it is true, unite together so as to form a kind of membrane at the surface of the yolk, but, as before observed, the primitive groove and laminæ dorsales are developed in the substance of this layer of cells and not beneath it. And it is only at a later period of the development of the embryo, that anything like an investing membrane is formed over its exterior, and this consists simply of a layer of pavement epithelium. A like absence of investing membrane was also observed by him in the ova of the salmon.‡ So that either Reichert's account must be considered erroneous, or, it must be concluded, that, in its earliest stages of development, the embryo pursues a different course in frogs, than in other amphibia and than in fishes.

Further information relating to the development of the several parts of the embryo of amphibia and fishes, is contained under the "Development of Organs."

The information we are in possession of, in relation to the changes ensuing in the ovum of *Mammalia* § at this stage, is derived almost exclusively from observations made by Bischoff upon the ova of rabbits and bitches. Some few of the facts to be here mentioned have been already stated in Müller's Physiology|| but it will be necessary to repeat them in order to preserve the continuity of the account.

About the time at which the mammiferous ovum reaches the uterus, the process of division and subdivision of the yolk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular aspect,

* Müller's Physiology, p. 1521.

† Entwickelungs-gesch. der Geburtshelferkröte, p. 32.

‡ Hist. Nat. des Poissons, t. i. p. 48.

§ Respecting the development of Birds no new facts of importance have recently been added to our knowledge. A series of plates illustrating the changes which the embryo of the chick undergoes during its development have been published by Prof. M. P. Erdl. (Entwickelung des Menschen und des Hünchens im Eie. 2. Bd. Leipsic, 1845.)

|| pp. 1560-64.

instead of its late mulberry-like appearance. The ovum indeed appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum; its yolk consisting, apparently, of a confused mass of finely granular substance.* But on more careful examination it is found that these granules are aggregated into numerous minute spherical masses, each of which contains a clear vesicle in its centre, but is not, at this period, provided with an enveloping membrane, and possesses none of the other characters of a cell.† The zona pellucida, and (in the rabbit) the layer of albuminous matter surrounding it, have at this time the same characters as when at the lower part of the Fallopian tube.

Shortly after this, important changes begin to ensue. Each of the several globular segments of the yolk becomes surrounded by a membrane, and is thus converted into a cell, the nucleus of which is formed by the central vesicle, the contents by the granular matter originally composing the globule; these granules usually arrange themselves concentrically around the nucleus.‡ When the peripheral cells, which are formed first, are fully developed, they arrange themselves at the surface of the yolk into a kind of membrane, and at the same time assume a pentagonal or hexagonal shape from mutual pressure, so as to resemble pavement epithelium. As the globular masses of the interior are gradually converted into cells, they also pass to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yolk remains filled only with a clear fluid. By this means the yolk is shortly converted into a kind of secondary vesicle, situated within the zona pellucida, and named by Bischoff, "vesicula blastodermica."§ The similarity of the several parts of this process with those observed by Vogt to take place in the ova of the frog (page 77) is very striking, and it is probable that the series of changes in the one are exactly analogous to those in the other. While these changes are proceeding within the yolk, which is at the same time gradually increasing in size, the zona pellucida and the layer of albuminous matter outside gradually coalesce, and so form a single membrane, the external investment of the ovum, from which the chorion is shortly afterwards produced.

In consequence of these changes, the Mammiferous ovum, when examined at this period, is found to consist of two nearly transparent vesicles enclosed one within the other, but differing from each other in composition.|| The external vesicle, which in the rabbit is formed, as above noticed, by the coalescence of the zona pellucida and albuminous covering,

* Bischoff, Entwickelungs-geschichte des Kaninchen-eies, p. 85. † Op. cit. p. 86.

‡ Bischoff, op. cit. p. 92, and Entwick. des Hunde-eies, p. 65. § Op. cit. p. 90.

|| See the account given by Von Baer, Wagner, and others, who also describe the two coats of the ovum. Müller's Physiology, p. 1561.

in the bitch by the zona pellucida alone, is textureless, solid, but exceedingly fine and delicate. The internal vesicle, on the other hand, is formed, in the manner before described, of hexagonal cells; within each of which a nucleus is usually observed. This internal vesicle, or vesicula blastodermica, shortly after it is formed, undergoes a rapid increase in extent and thickness; its growth being effected apparently by the development of new cells. Concerning the mode in which these new cells are developed, however, Bischoff cannot speak with certainty, though having observed that while the growth of the vesicula blastodermica proceeds, the granules within the already formed cells gradually diminish in number, he thinks it not improbable that these granules are employed in the production of new cells, and that possibly each granule constitutes a nucleus, around which a fresh cell is developed;* but he has never witnessed anything resembling the development of one cell within another, and he considers it very questionable if this mode of multiplication is ever pursued in the yolk.

Very soon after its formation, the vesicula blastodermica presents at one point on its surface an opake roundish spot, which is produced by an accumulation of cells and nuclei of cells, of less transparency than elsewhere. This space, the "area germinativa" (Fruchthof), is the part at which the embryo first appears. It was supposed by Reichert,† that in the chick, and also in Mammalia, the appearance of this, the first trace of the embryo, was preceded by the formation, at the surface of the yolk, of an investing membrane, beneath which the area germinativa is formed, but Bischoff shews that certainly in Mammalia (as Vogt also shewed to be the case in amphibia and fishes, page 80), no such investing membrane exists, and that the area germinativa is formed upon the surface of the germinal membrane and covered only by the zona pellucida, or external membrane of the ovum as it has now become.‡

Bischoff has also found § that the germinal membrane of the Mammiferous ovum presently becomes divided into two distinct laminæ, in the same manner as has been long known to take place in the ova of birds.|| This division is at first most manifest at the situation of the area germinativa, but it soon extends from this point and implicates nearly the whole of the germinal membrane. Bischoff has adopted for these laminæ the same names that are applied to them in the chick, namely, for the external one, the serous, or animal layer; for the internal one, the mucous, or vegetative layer. He has not been able to find the third layer described by Reichert as existing in the ova of the chick, and called by him membrana intermedia.¶

* Entwickelungs-geschicte des Hunde-eies, p. 66. † Müller's Physiology, p. 1543.

‡ Entwickelungs-geschichte des Hunde-eies. p. 68.

§ Entwickelungs-geschichte der Säugethiere und des Menschen. Leipsic, 1842, p. 59.

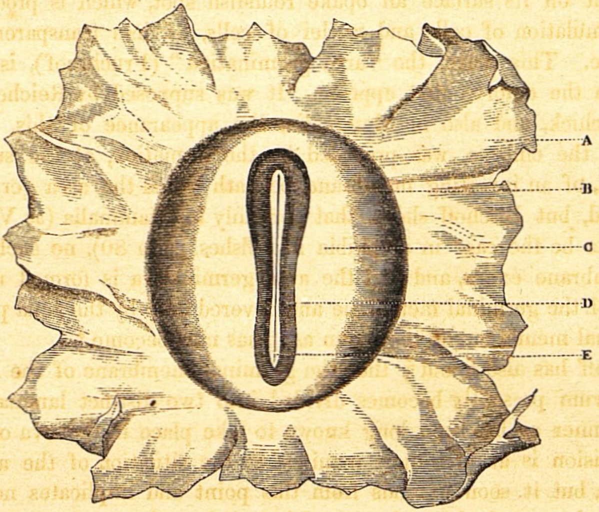
|| Müller's Physiology, p. 1533. ¶ Müller's Physiology, p 1544.

OF THE DEVELOPMENT OF THE EMBRYO.

1. *In Mammiferous Animals.**

From the observations of recent embryologists, especially of Professor Bischoff,† it would appear that in the earlier periods of its formation the Mammalian embryo presents a close resemblance to the embryo of the chick, and that (as was shewn by Prévost and Dumas)‡ the process of development in each takes place according to the same general plan. We have already traced the changes which ensue in the Mammiferous ovum subsequent to impregnation, as far as the formation of the area germinativa, and the separation of the germinal membrane into two layers. At its first appearance the area germinativa has a rounded form, but it soon loses this and becomes oval, then pear-shaped, and while this change in form is taking place, there gradually appears in its centre a clear space or area pellucida

Fig. 10.§



(fig. 10, C), bounded externally by a more opaque circle which subsequently becomes the area vasculosa (B). In the formation of these two spaces, both the serous and mucous laminæ of the germinal membrane take

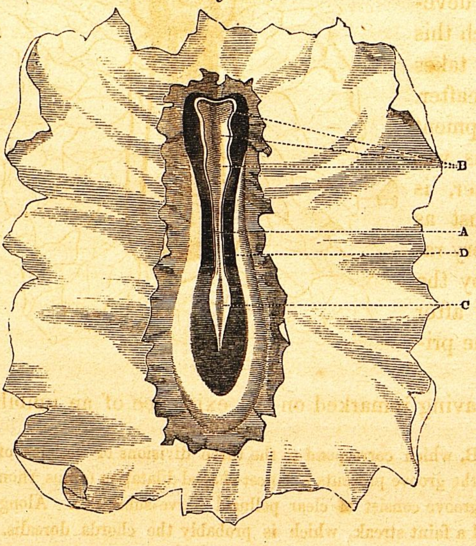
* Chapter iii. p. 1560 of Müller's Physiology. † Operibus citatis.

‡ Müller's Physiology, p. 1566.

§ Fig. 10. Portion of the germinal membrane of a bitch's ovum, with the area pellucida and rudiments of the embryo; magnified ten diameters. A. Germinal membrane. B. Area vasculosa. C. Area pellucida. D. Laminæ dorsales. E. Primitive groove, bounded laterally by the pale pellucid substance of which the central nervous system is composed. After Bischoff. (Entwickelungs-geschichte des Hunde-eies.)

part. The comparative obscurity of the outer space—the area vasculosa—is due to the greater accumulation of nucleated cells and nuclei at that part than in the area pellucida. The first trace of the embryo in the centre of the area pellucida, consists, not of a projecting line, as described by Von Baer, but of a shallow groove (E), as shewn especially by Reichert in the embryo of the chick.* This is formed in the external or serous fold alone of the germinal membrane: the mucous fold having no direct share in its production. Coincidently with the formation of the primitive groove, two oval masses, the laminæ dorsales (D) appear, one on each side of the groove. Their form changes according as does that of the area pellucida: passing gradually with the latter from an oval to a pyriform shape, and eventually becoming guitar-shaped. The upper borders of these two masses gradually tend towards each other, as in the embryo of the chick, and ultimately unite, so as to convert the primitive groove into a canal or tube. But with regard to the mode in which these masses unite, and to their own nature, and the changes which ensue in them, Bischoff maintains a different view to that advocated by Reichert. The latter physiologist supposed that, at least in the chick and in the frog, these oval masses constitute the rudimentary parts of the central nervous system, but Bischoff is of opinion with Von Baer, that in Mammalia they are the foundations of the dorsal part of the trunk of the embryo, while the nervous system is developed, as will be hereafter more fully described, only from their most internal part, that, namely, which forms the bottom and sides of the primitive groove. Shortly after, or, as shewn in fig. 11 from a bitch's ovum, even before the laminæ dorsales have closed over the primitive groove, a few square-shaped, at first indistinct, plates, which are the rudiments of vertebræ (fig. 11, D), begin to appear at about the middle of each. It is not possible to perceive at this time the chorda dorsalis so distinctly observed in birds and fish; but later, when the bodies of the

Fig. 11.†

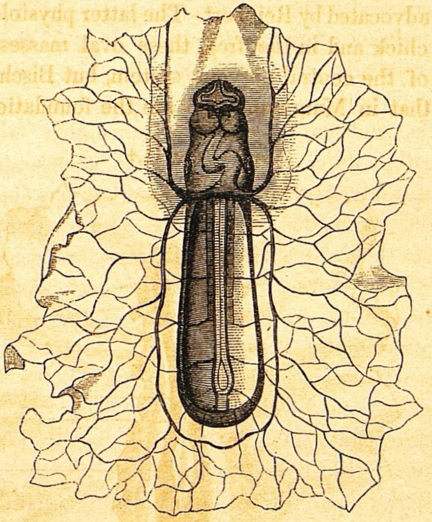


* Müller's Physiology, p. 1547.

† Fig. 11. Portion of the germinal membrane, with rudiments of the embryo from the ovum of a bitch. The primitive groove, A, is not yet closed, and at its upper or cephalic

vertebræ have begun to be formed, an appearance of a chorda in their centre is perceptible. The two laminæ viscerales or ventrales, which, as described by Von Baer, are also formed in the serous fold, and proceed from the laminæ dorsales, continue at first on the same plane with the germinal membrane, and only by degrees bend downwards and inwards towards the cavity of the yolk, where they unite and form the anterior walls of the trunk. While the borders of the primitive groove are approaching each other and about to close, the groove itself at its anterior extremity dilates into three recesses or vesicles (fig. 11, B), which, with the nervous matter developed in them, constitute the rudimentary brain; at the same time, the surrounding parts assume the characters of the head of the embryo which raises itself above the surface and bends forwards and downwards as in the chick. During the development of the above parts of the embryo, an accumulation of cells takes place between the two laminæ of the germinal membrane at the area vasculosa. These cells shortly form themselves, as in the bird, into a distinct layer—the vascular lamina—which serves as a groundwork in which the first blood-vessels of the embryo are developed. The mode in which this development of vessels takes place will be described hereafter.

Fig. 12.*



Amnion.—The development of the amnion, which, as was pointed out by Von Baer, is effected in Mammalia just as in birds, takes place very rapidly, being completed by the end of twenty-four hours after the first appearance of the primitive groove.†

Umbilical vesicle. — Having remarked on the existence of an umbilical

end presents three dilatations, B, which correspond to the three divisions or vesicles of the brain. At its lower extremity the groove presents a lancet-shaped dilatation (sinus rhomboidalis) C. The margins of the groove consist of clear pellucid nerve-substance. Along the bottom of the groove is observed a faint streak, which is probably the chorda dorsalis. D. Vertebral plates. After Bischoff. (Ibid.)

* Fig. 12. Embryo from a bitch at the 23d or 24th day, magnified ten diameters. It shews the net-work of blood-vessels in the vascular lamina of the germinal membrane and the trunks of the omphalo-mesenteric veins entering the lower part of the S-shaped heart. The first part of the aorta is also seen. After Bischoff. (Ibid.)

† Bischoff, Entwick. der Säugeth. und des Menschen, p. 108.

vesicle in the embryos of all Mammalia yet examined, on its being invariably situated on the outside of the body of the embryo, and on its disappearance in all, either before, or at the termination of intra-uterine life, Bischoff * confirms the observations of Von Baer and Coste,† that in its ulterior relations to the embryo this vesicle presents considerable varieties in the different classes of Mammalia. In ruminants and pachyderms, although at its first formation the umbilical vesicle grows with extreme rapidity, yet very shortly its development is arrested, and it then begins to disappear. In the embryos of cows not more than six lines long, the middle portion alone is found still in existence, and its attachment to the intestine consists no longer of a canal, but only of a thread-like pedicle. Its blood-vessels also have undergone a proportionate reduction. In the pig an almost equally early disappearance of the vesicle is observed. In Carnivora, on the contrary, the umbilical vesicle remains during the whole period of intra-uterine existence; presenting itself as a cylindrical sac, the surface of which is throughout abundantly supplied with omphalo-mesenteric vessels, and the cavity of which is long in direct communication with that of the intestine. The left side of the vesicle is covered by the allantois, while its right side is in contact with the chorion. At a certain period the vesicle surrounds the upper part of the embryo in such a manner that this part appears as if contained within its cavity, and has been so described by some embryologists. But at a later period when the embryo has detached itself from this relation to the vesicle, the error of such a supposition is rendered manifest. In rodents, the rabbit for example, the umbilical vesicle also persists during the whole of intra-uterine life, and at one period there is observed a similar deceptive appearance as in Carnivora, of the embryo being contained within the cavity of the vesicle.

Allantois.—According to Bischoff,‡ the allantois of the Mammalian embryo is developed neither from the intestinal tube, as stated by Von Baer, Rathke, Valentin, and others, nor from the Wolffian bodies, as was said by Reichert,§ to be the case in the chick; for at the time of its first appearance no trace either of the intestinal canal or of the Wolffian bodies can be perceived. At its earliest appearance, the allantois in the rabbit consists of a solid mass of cells projecting from the visceral plate of the tail. But in the dog this mass is at first double (figs. 13 and 14), though the two halves soon fuse together, and are converted into a single vesicle. The allantois is abundantly vascular, for it contains the ramifying extremities of the two arteries which run along the sides of the vertebral arches, and of the two veins which are situated within the walls of the visceral laminæ. These vessels subsequently become the umbilical arteries

* Op. cit. p. 113. † Müller's Physiology, p. 1570.

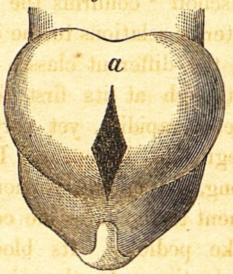
‡ Entwick. der Säugeth. und des Menschen, p. 116; and Entwick. des Kaninchen-eies, p. 122.

§ Müller's Physiology, p. 1554.

and veins. When the allantois has assumed the form of a vesicle, it then communicates both with the intestinal tube and the corpora Wolffiana,

Fig. 13.*

Fig. 14.†



though the mode in which this communication is effected is not quite clear. The allantois now rapidly increases in size, and the two umbilical arteries in connection with it are recognised as branches of the iliac, while the umbilical veins unite into either one or two trunks, which empty themselves in the liver and the inferior vena cava. As the visceral laminæ close in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions, the smaller of which is retained in the abdomen, and is converted into the urinary bladder, while the external and larger portion, accompanied by the umbilical vessels, proceeds to the chorion, where its vessels are brought into connection with those developed within the villi of this structure. The middle portion of the allantois, that, namely, which traverses the umbilicus, at first contracts into a canal, and subsequently is converted into a fibrous cord, the urachus.‡ The different modes in which the allantois is subsequently disposed of in the different orders of Mammalia, are described by Bischoff almost as they were by Von Baer,§ whose account Bischoff for the most part confirms.

The development of the other parts of the Mammalian embryo will be considered under the "Development of Organs," for, to avoid repetition, it is deemed advisable to combine in one general account all the new information on this subject, which has been obtained from observations on different classes of animals.

* Fig. 13. The lower part of the body of a bitch's embryo, magnified 10 diameters. The mucous and vascular layers of the germinal membrane are turned back to shew (*a*) the pedicle of the umbilical vesicle at its entrance into the abdominal cavity. *b. b.* Two cellular masses out of which the allantois is formed. After Bischoff.

† Fig. 14. The lower extremity of an older embryo. The allantois *a* is developed into a single vesicle, but its origin from two symmetrical halves is still shewn, especially by the fissure in the middle. (Ibid.)

‡ See Langenbeck's Account of the Allantois in the Human Ovum, on the next page.

§ Müller's Physiology, p. 1570.

2. *In the human subject.**

Allantois.—Bischoff † inclines to the same view of the development and office of the allantois of the human embryo, as was maintained by Professor Müller ‡ and many other embryologists, namely, that, as is the case in the embryo of rodent animals, it is developed merely as a narrow vesicle which elongates itself till it reaches the chorion, and is only destined to conduct the umbilical vessels to that structure, having done which, it disappears, the urachus of the urinary bladder being its only remains. In further refutation of the opinion of Velpeau and other anatomists who consider that after its formation, the allantois increases rapidly, and as in ruminants, surrounds the embryo together with its amnion and umbilical vesicle, uniting by one of its layers with the chorion, by the other with the amnion, Bischoff draws attention to three principal circumstances which are opposed to this view. First, no one has yet observed the smallest trace of the allantois, either on the internal surface of the chorion, or on the external surface of the amnion; both the chorion and amnion are perfectly simple membranes. Secondly, in all cases in which the allantois applies itself upon the other membranes of the embryo, it furnishes these with vessels, so that in pachyderms, ruminants, and Carnivora in which the allantois is thus disposed, the chorion and amnion are at a certain period, richly supplied with vessels; but in the human ovum nothing like this occurs, no vessels at any period of its existence are ever found in either of these membranes, except at that part where the allantois comes into contact with the chorion and at which the placenta is subsequently developed. Thirdly, if, as assumed, the allantois in its development passes at all parts between the chorion and amnion, it must necessarily invest the umbilical vesicle, on one side or the other; but this is never found to be the case.

So far as concerns the refutation of Velpeau's hypothesis, the account of the human allantois recently published by Dr. Max Langenbeck § accords with that of Bischoff. But Langenbeck has proceeded further and has given a more satisfactory explanation of the probable nature and ultimate condition of this structure than has been afforded by any previous physiologist. His researches shew that the allantois at an early period comes into immediate relation with the Wolffian bodies—in this agreeing with Reichert in his observations on the chick || and, moreover, is concerned more directly, and in a different manner than has yet been described, in the formation of the urinary bladder. At its first development the allantois of the human embryo appears, as has been described by others, in the form of

* Müller's Physiology, p. 1572.

† Entwick. der Säugeth. und des Menschen, p. 129.

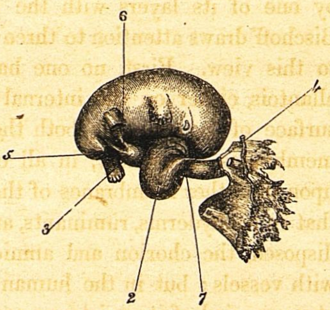
‡ Physiology, p. 1582.

§ Untersuchungen über die Allantois. Göttingen, 1847.

|| Müller's Physiology, p. 1554.

a somewhat pear-shaped body protruding from the pelvic portion of the trunk, and soon becomes vesicular. Shortly after its formation there is observed a narrowing of that portion of the vesicular body nearest the fœtus, (fig. 15, 3) while the more distant portion undergoes a rapid increase in size, and gradually approaches the chorion, to which structure the numerous vessels surrounding the allantois are thus conducted from the body of the fœtus. This object attained, the development of the allantois is completed, and the subsequent changes which it undergoes appear to be retrograde ones. The first of these changes which ensues is the production of a kind of twist or constriction on that side of the vesicular part of the allantois turned towards the chorion (fig. 15, 7); this is the commencement of the formation of the urachus. The vesicular part constitutes the rudiment of the urinary bladder, and maintains its connection with the body of the embryo by means of the narrowed tubular part (3) already alluded to (and which has been hitherto, but erroneously, described as the urachus). This tubular part, indeed, forms a direct communication between the urinary bladder and the primordial kidneys or Wolffian bodies, by dividing into two portions, each of which passes directly into the corresponding Wolffian body, and thus the ureters are formed.† As the embryo increases in size, and the Wolffian bodies gradually disappear to be replaced by the kidneys, the ureters together with the urinary bladder—which by degrees loses its round or elliptical form to be elongated in the direction corresponding to the length of the umbilical cord—are drawn into the cavity of the pelvis. When this has occurred the bladder assumes a club-shaped form, the base of which represents the fundus of the organ, while the apex tapers upwards to pass into the urachus, which for some little distance is therefore tubular. Langenbeck cannot speak with certainty respecting the length of time required for the bladder to be thus drawn into the body of the embryo; but he considers that by the twentieth week the process is always completed, frequently even by the twelfth. For long after this period, however, the

Fig. 15.*



* Fig. 15. Human fœtus with the umbilical cord, allantois, and a portion of the chorion. After Langenbeck. The right hind extremity has been removed. 2. Allantois (or rudiment of the urinary bladder). 3 and 4. Umbilical cord. 5. Ureters. 6. Ductus vitello-intestinalis. 7. Fold or constriction of the allantois, indicating the first formation of the urachus.

† This division and the junction of the branches with the extremities of the Wolffian bodies, has been observed also by Professor Budge in a five-weeks old human embryo. (Müller's Archiv. 1847, p. 9.)

portion of the urachus between the bladder and the umbilicus remains tubular, and in some instances it continues permanently in that condition, so that urine can escape from the umbilicus.*

Amnion.—M. Serres† has again maintained that the amnion of the human embryo, instead of being produced by a fold of the external layer of the germinal membrane rising up and gradually enveloping the embryo, is originally an independent vesicle outside the embryo, and that the latter connects itself with it by dipping into, and eventually completely enveloping itself with it. This view has been supported also by MM. Maignien and Jacquart,‡ from the appearances presented by an early aborted embryo; but from Bischoff's§ account it would seem that both these observers as well as M. Serres must, in the specimens examined by them, have overlooked the true amnion, which from the early age of the embryos or from some morbid change may have been obscured, and probably mistook for it either the allantois or the umbilical vesicle. In his work on embryology,‖ Bischoff states the various arguments in favour of the view that the amnion of the human ovum observes the same mode of development as obtains in other Mammifera.

Chorion.—Little requires to be said of the chorion of the human ovum. It does not appear to present any essential difference from the chorion of other Mammalia. Its formation around the ovum in rabbits and bitches has been already described. In the former animals it is developed apparently from the zona pellucida and the layer of albuminous matter by which the zona is surrounded; but in the bitch, in which no such albuminous deposit occurs, it is developed (according to Bischoff) from the zona pellucida alone. Bischoff believes that the human ovum, like that of the bitch, is unprovided with an albuminous covering, and that the chorion in this case also is formed directly from the zona pellucida; but Mr. Wharton Jones is inclined to doubt this statement. The villi of the chorion, as stated elsewhere, are, at their first appearance, composed entirely of cells, and it is not until the arrival of the allantois at the chorion, that vessels are developed within them.

Formation and structure of the decidua.—The subject of the formation and structure of the membrana decidua, has within the last few years been investigated anew by several physiologists, and the general tendency of

* An account of the early development of the allantois of the human ovum is furnished by M. Serres (An. des Sc. Nat. 1843; and Gazette Med. de Paris, 1843, p. 414), but it contains nothing essentially new. Serres is of the same opinion with Langenbeck concerning the close relation subsisting between the allantois and the corpora Wolffiana. For Coste's view of the human allantois, *vide* Gaz. Med. 1843, p. 696; and for that of Velpeau and others, see the account in the same journal of the discussion which ensued among the members of the Academy of Sciences, after the reading of M. Serres's memoir.

† Gazette Médicale, Juin, 1843.

‡ Gaz. Med. Novembre, 1843.

§ Müller's Archiv. 1844, Jahresbericht, p. 144.

‖ Op. cit. p. 132 *et seq.*

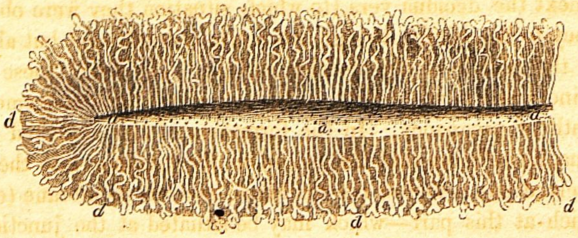
the results obtained by them is to confirm the opinion of Dr. Sharpey and of Prof. E. H. Weber, stated at page 1574 of Müller's Physiology, that this membrane is not a structure of new formation, but is produced simply by an increased development of the parts composing the mucous membrane of the uterus, and of an increased quantity of matter secreted by the follicles of this membrane. In further support of this opinion, E. H. Weber* has contributed some additional particulars relating to the mode of formation of the decidua, and the ultimate destination of its several parts. They do not, however, throw much further light on the subject than was already afforded by the researches of Dr. Sharpey. Many of the observations of the latter physiologist, Weber amply confirms. He corroborates, for example, all that was stated by Dr. Sharpey concerning the existence and peculiarities of the two sets of glands found in the mucous membrane of the bitch's uterus, and of the changes which ensue in these glands after conception. The only point in which, on this subject, Weber's account differs from that of Dr. Sharpey, is in describing the vascular processes of the chorion as sending off their branches within the glands of the mucous membrane of the uterus, and carrying the lining membrane of the glands with them in folds which they form around the maternal vessels, whereas Dr. Sharpey states that the fœtal processes send off their branches outside the uterine glands, and describes the expanded summits of these processes which close the mouths of the glands, as being "smooth and even, and covered with a prolongation of the same epithelium which lines the cells"—or dilated parts of the glands. Dr. Sharpey also describes these glands as remaining during pregnancy, and secreting a fluid which is probably absorbed by the fœtal vessels as nutriment for the fœtus; but, according to Weber's account, these glands, or, at least, the dilated or cell-like portions of them, entirely disappears as the fœtal blood-vessels come into relation with those of the mother. Professor Weber confirms Dr. Sharpey's description of the simple follicles observed on the mucous membrane of the human uterus immediately after impregnation. He could never observe that these follicles formed dilated pouches previous to opening upon the surface of the uterus, as in the bitch, or that at their opposite extremity they branched or even divided into two trunks; but he noticed that at their termination in the substance of the uterus, they frequently formed two or three closed sacculi. (See fig. 16, p. 92.) He states that he could never perceive the villi of the chorion to enter the orifices of these glands, although Bischoff† (whose account of the uterine glands and of the membrana decidua, in other respects corresponds closely with the descriptions given by Dr. Sharpey and Professor Weber) considers it probable that they do. The existence of these simple glands in the mucous mem-

* Zusätze zur Lehre vom Baue und den Verrichtungen der Geschlechtsorgane. Leipzig, 1846.

† Müller's Archiv. 1846, p. 112.

brane of the unimpregnated human uterus, appears to have never yet been clearly demonstrated, although their appearance immediately after impregnation and the existence of them in the unimpregnated uterus of the bitch,

Fig. 16.*



and many other animals, renders it highly probable that in the human uterus also they exist previous to impregnation, although of such minute size that they have hitherto escaped detection.

According to the account furnished by Weber, and that given by the other physiologists who have written on the subject, the mucous membrane of the uterus immediately after conception becomes swollen and soft, the cilia of its epithelial cells disappear (Weber),† its tubular glands and the vascular network occupying the spaces between them increase considerably in size, whilst, as shewn both by Professor Weber and Professor Goodsir,‡ a substance composed of nucleated cells fills up the inter-follicular spaces in which the bloodvessels are contained. To this inter-follicular substance Professor Goodsir attributes much of the increased thickness of the mucous membrane, and he considers that it plays an important part in the further purposes of the decidua. When thus developed, the mucous membrane of the uterus, according to Professor Goodsir, begins to secrete largely, and the cavity of the uterus is shortly filled with the secreted fluid which constitutes the "hydroperione" of Breschet. The portion of this secretion by which the os uteri is plugged up, is composed of elongated epithelial cells; whilst the portion which immediately surrounds the ovum consists of cells of a spherical form. To these latter cells Professor Goodsir attributes an important office, that, namely, of preparing nutritive material for the ovum by their further development and the production of successive quantities of new cells.

It is of these cells also, according to the same observer, that the decidua reflexa is formed, and not, as was formerly supposed, by the ovum protrud-

* Fig. 16. Section of the lining membrane of a human uterus at the period of commencing pregnancy, shewing the arrangement and other peculiarities of the glands *d. d. d.*, with their orifices, *a. a. a.*, on the internal surface of the organ. Twice the natural size. After E. H. Weber.

† Froriep's N. Notizen, No. 507, p. 1, 1842.

‡ Anatomical and Pathological Observations, Edinburgh, 1845.

ing into and carrying before it a portion of the decidua vera on its entrance into the uterus. But E. H. Weber * is of opinion that the decidua reflexa is really formed of a layer or reflection of the decidua vera, and he considers his opinion to be supported by the fact, that in very small ova, minute openings, apparently of the uterine follicles, are found not merely at the margins next the decidua vera (to which situation they were observed by Dr. Sharpey to be chiefly, though not entirely, confined),† but also extend as far as the middle of the decidua reflexa. He found these openings quite distinct even in an embryo examined at the commencement of the third month of pregnancy. In the formation of this reflected portion of the decidua, he believes that the ovum on its entrance into the uterus, is either received into a fold of the thickened mucous membrane (or decidua vera), which at this part—which may be situated at the junction of the Fallopian tube to the uterus, or in the anterior or posterior wall of this organ—is more developed than elsewhere, and that as it enlarges it carries along with it a covering of this membrane in the manner suggested by Dr. Sharpey; ‡ or that it becomes simply invested by a superficial layer of the decidua vera, which at the point where the ovum comes in contact with it, separates from the deeper portion and carries with it apertures corresponding to the orifices of the uterine glands—just as cuticle raised by a blister bears with it the openings of the sudoriferous ducts. A view somewhat similar to the first of these appears to be entertained also by M. Coste.§

Formation and Structure of the Human Placenta.||

A very complete account of the structure of the human placenta, has been given by Professor Goodsir:¶ his paper has been already referred to, but it now requires a more detailed notice. In many respects his description agrees with that furnished by Professor Weber, Dr. Reid, and Mr. Dalrymple, as contained in Müller's Physiology.** The existence of two distinct portions in the placenta, the one belonging to the fœtus and the other to the parent, is clearly shewn, and he finds that the communication between these two portions is effected by means of nucleated cells.

As already stated, Professor Goodsir considers the decidua reflexa to be formed of a number of cells secreted by the enlarged follicles of the mucous membrane of the uterus; that these cells possess the power of further development and of multiplication; and that eventually they completely surround the chorion, to the absorbing villi of which they supply nutritive material for the embryo. At the earliest period of

* Op. cit. p. 35.
† Müller's Physiology, p. 1580.
‡ Müller's Physiology, p. 1580.
§ Comptes Rendus, 24 Mai, 1847, p. 893.
|| Müller's Physiology, chapter iv. p. 1604.
¶ Op. cit. p. 50.
** P. 1604, *et seq.*

their formation the villi of the chorion consist of nucleated cells, bounded externally by a fine transparent membrane, and are immersed in the substance of the cellular decidua reflexa, from which they absorb nutriment for the embryo. When, however, the embryo has attained a certain stage of development, at which the allantois containing the umbilical vessels arrives at the internal surface of the chorion, and at which blood-vessels are also formed within the villi * and communicate with the umbilical vessels, the villi at that part which is to be converted into the placenta, increase in number and in size, and come into relation with the vascular system of the mother. At this period each villus contains one or more loops of blood-vessels, its cells are diminished in quantity, but a few are always found at its terminal extremity, and it still possesses its external investing membrane. Meanwhile the vessels of the decidua vera, or highly-developed mucous membrane of the uterus, enlarge, and "assume the appearance of sinuses encroaching on the space formerly occupied by the cellular decidua, in the midst of which the villi of the chorion are imbedded. This increase in the calibre of the decidual capillaries goes on to such an extent that finally the villi are completely bound up or covered by the membrane which constitutes the walls of the vessels, this membrane following the contours of all the villi, and even passing to a certain extent over the branches and stems of the tufts." In this manner, as was shewn by Dr. J. Reid, Weber, and other observers,† the tufts and villi of the fœtal portion of the placenta are completely ensheathed by the lining membrane of the vascular system of the mother. Between this membrane of the enlarged maternal vessels, and the membrane of each villus, there still remains a layer of nucleated cells of the decidua, (fig. 17 *b*), which the enlarging vessels have carried before them. These cells, at certain parts of the circumference of the villus, are grouped together in greater quantities, and appear to be passing off from a spot in the centre of the mass (*c*); each such group constitutes what Professor Goodsir calls a germinal spot, or nutritive centre, whose office appears to be to supply a constant succession of new cells in the place of those which are rapidly disappearing in the performance of the functions of the villus.

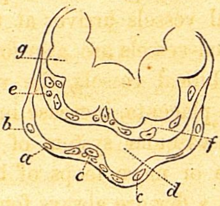
It appears, therefore, that, at the villi of the placental tufts, where the fœtal and maternal portions of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated

* This formation of blood-vessels within the villi appears to take place quite independently of any communication with the vessels of the embyro, with which they only subsequently unite (Bischoff, Entwick. der Säugeth. und des Menschen, p. 127); it is probably effected through the transformation of the cells of the villi, in a manner which will be pointed out hereafter when speaking of the mode of development of blood-vessels generally.

† Müller's Physiology, p. 1606. See also Weber's Zusätze der Geschlechtsorgane, p. 41.

cells, one of which belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the parent the materials destined for the blood of the fœtus, while the other belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and probably serves for the absorption of the material secreted by the other set of cells, and for its conveyance into the blood-vessels of the fœtus. In describing these several membranes and layers of cells as composing each placental villus, Professor Goodsir calls the lining membrane of the vascular system of the mother the external membrane of the villus (fig. 17 *a*), the layer of cells between this and the villus, the external cells of the villus (*b*), the membrane within these, the internal membrane of the villus (*e*), and the cells between this and the loop of vessels, the internal cells of the villus (*f*). Between the two sets of cells with their investing membrane there exists a space (*d*,) into which it is probable that the materials secreted by the external cells of the villus are poured, in order that they may be absorbed by the internal cells, and thus conveyed into the fœtal vessels. As the decidual vessels enlarge and extend themselves, so as to ensheath the placental tufts, their lining membrane forms numerous folds, the venous reflections of Dr. Reid, which pass from tuft to tuft, and villus to villus, connecting them together in the same manner as the intestines are tied together and held down in various places by reflections of the peritoneum. These folds or processes of the venous membrane appear in the form of innumerable threads passing from the sides or apex of one villus to that of another throughout the substance of the placenta. On minute examination, Professor Goodsir found that these threads were tubular, and that the membrane of which they were formed was distinctly continuous in one direction with the lining membrane of the enlarged decidual vessels, and in the other with the external membrane of the placental villi, forming, therefore, in this way, the central containing membrane of the bag of the placenta. The tubular portion of the threads was filled with cells, which were continuous in one direction with the cells of the placental decidua, in the other with the external cells of the villi. (See fig. 18, p. 96.)

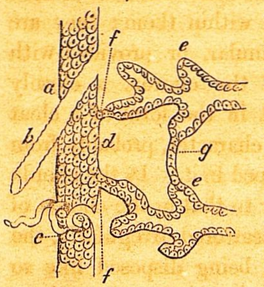
Fig. 17.*



* Fig. 17. Extremity of a placental villus. *a*. External membrane of the villus, or lining membrane of the vascular system of the mother. *b*. External cells of the villus. *c c*. Germinal spots or centres of the external cells. *d*. Space between the maternal and fœtal portions of the villus. *e*. Internal membrane of the villus, or external membrane of the chorion. *f*. Internal cells of the villus, or cells of the chorion. *g*. Loop of umbilical vessels. After Goodsir.

Several varieties as to the mode of arrangement of the tuft of umbilical vessels in the villi are described by Professor Goodsir. The general rule is that one umbilical vessel enters a villus, forms a simple, more or less open loop, and passes out again without dividing. Occasionally the vessel divides, and its branches either pass out separate or anastomose into a single trunk again. Sometimes more than one vessel enters a single villus, which either divide into other branches, or leave the villus as they entered. Professor Goodsir confirms the fact observed by Professor Weber and Mr. Dalrymple,† that the same vessel may enter and retire from two or more villi before it becomes continuous with a vein.

Fig. 18.*



OF THE DEVELOPMENT OF ORGANS.‡

Development of the vertebral column and cranium.§

Chorda dorsalis.—A very minute account of the structure of the chorda dorsalis in Amphibia and fishes, and of the metamorphoses undergone by it, and by the surrounding cellular substance, in the formation of the several parts of the vertebral system, has been furnished by Vogt,‖ from observations made principally on the toad (Alytes obstetricans) on Tritons, and on the salmon (Coregonus palæa). In the former of these animals he observed, that at its earliest formation the chorda dorsalis contains no cells, being composed of a clear gelatinous-looking substance, with which are mingled, without any definite arrangement, numerous molecular bodies and a few plates of stearine. Shortly, numerous scattered roundish cells appear, consisting of a fine membrane, enclosing a pellucid gelatinous-looking fluid, and unprovided with a nucleus. They are formed at first at the cephalic extremity of the chorda, but soon mul-

* Fig. 18. " A diagram illustrating the arrangement of the placental decidua. *a.* Parietal decidua. *b.* A venous sinus passing obliquely through it by a valvular opening. *c.* A curling artery passing in the same direction. *d.* The lining membrane of the maternal vascular system (external membrane of villus) passing in from the artery and vein lining the bag of the placenta and covering (*e e*) the fœtal tufts, passing on to the latter by two routes, first by their stems from the fœtal side of the cavity, secondly by the terminal and decidual bars (*f f*) from the uterine side, and from one tuft to the other by the lateral bar (*g*)." Throughout its whole course, except along the stems of the tuft, and the fœtal side of the placenta, this membrane is in contact with decidual cells. After Goodsir.

† Müller's Physiology, p. 1605.

‡ Section iii. chap i. p. 1609 of Müller's Physiology. § Page 1610.

‖ Entwick. der Geburtshelferkröte, pp. 41 *et seq.*; and Histoire Naturelle des Poissons d'eau douce, by M. Agassiz, t. i.: works already quoted from.

tiply so rapidly, that in a short time the substance of the chorda is composed almost entirely of them, the granular matter being reduced to a small quantity of intercellular substance. As the cells increase in size, clear, flat, vesicular nuclei are shortly developed within them; they are sometimes central, sometimes parietal, never granular, or provided with a nucleolus. Around the cellular substance of the chorda, a closely fitting sheath is early developed; it appears first in the form of a clear pellucid fluid, but subsequently assumes a fibrous character, probably from the transformation of cells which are shortly developed in it. In the chorda of the Triton Lobatus, a granular substance similar to that in the chorda of the toad, is first observed; but instead of being scattered irregularly, the granules have a somewhat circular arrangement, being disposed like so many rings around the chorda. As in the toad, so also in the triton, these granules shortly disappear, and are replaced by cells, the formation of which presents itself first at the cephalic extremity, and rapidly extends through the whole length of the chorda. Like the granules which preceded them, these cells in the triton observe an orderly arrangement; each cell having a size equal to the diameter of the chorda, and, being flattened by the pressure of the adjoining cells, contributes in giving to the chorda the appearance of being composed of a linear series of rings enclosed within its fibrous sheath. The cells lie close to each other, very little intercellular substance being present. At a later period of the larval life of the triton, this regular arrangement of the cells is somewhat modified. The diameter of many parts of the chorda, instead of being occupied by only one nucleated cell, now presents two or three of about equal size.

Concerning the origin of the finely granular material of which the chorda is at first composed, and from which the cells are developed, Vogt is of opinion that it is furnished by embryonic cells. He considers that along the line to be subsequently occupied by the chorda dorsalis, are deposited embryonic cells similar to those from which all other organs of the embryo are formed: that the membranous walls of these cells shortly disappear, and that the cell contents thereby liberated constitute the granular matrix or cytoblastema from which the second set of cells of the chorda are formed.* Kölliker,† however, appears to be of opinion that the cells of the chorda dorsalis are produced directly from the primary embryonic cells which simply enlarge, and at the same time lose the granular matter which they originally contained. According to Prevost and Lebert,‡ again, they are formed from the enlarging nuclei of the embryonic cells. The development of the chorda dorsalis in the embryo of the salmon (Corego-

* This is in accordance with his opinion, again to be mentioned, that none of the embryonic tissues are developed directly from the first embryonic cells, but that these cells invariably resolve themselves into a secondary blastema, out of which are formed new cells, which give rise to the tissues of the embryo.

† An. des Sc. Nat. 1846, p. 92. ‡ An. des Sc. Nat. 1844, p. 206.

nus palœa) was found by Vogt * to pursue an almost similar course to that observed in the toad and triton. Very large cells are early observed in the position occupied by the chorda; these shortly disappear, leaving a transparent, faintly granular substance, from which the subsequent cells of the chorda appear to be produced.

Vertebral column.—The nature of the changes undergone by the fibrous sheath of the chorda dorsalis of Alytes obstetricans, by which the development of the bodies of the vertebræ is effected, has also been minutely investigated by Vogt. In the first "laying down" of the individual segments of the vertebral column, the sheath of the chorda dorsalis can exercise no share, for, at the period at which this occurs, the sheath is not yet formed from that part of the substance of the chorda to which it owes its origin. From the time of its first appearance, however, the sheath becomes so intimately connected with the mass of cell-substance surrounding it, that it can at no time be completely separated therefrom. The first trace of solidification of the divisions of the vertebral column is observed immediately external to the sheath of the chorda: and presents itself in the form of cartilaginous rings adherent internally to the sheath, and externally to the surrounding cell-substance, which gradually assumes the characters of muscular tissue. At first, the lines of separation between the muscular, cartilaginous and fibrous layers of which the vertebral system is at this time composed, are very obscure; but, shortly, the distinction between the two former becomes manifest, while, between the cartilaginous layer and the fibrous sheath of the chorda, no line of demarcation can ever be perceived even with the aid of the microscope. Indeed these two latter tissues merge insensibly one into the other, so that in fragments of the sheath examined beneath the microscope, cartilage-cells may be observed scattered throughout its fibrous structure. Eventually this fibrous structure entirely disappears, and the whole sheath becomes cartilaginous; being thus converted, by change of tissue, into the bodies of the vertebræ. This account is in accordance with the observation made by Professor Müller,† that in some of the frog-like Amphibia and the Salamandrinæ, the ossification of the vertebræ takes place in the sheath of the cord. Coincident with the conversion of the sheath into cartilage, and the encroachment of this on the substance of the chorda, the cells of this substance gradually disappear and eventually are found only in the spaces between the bodies of the vertebræ. They are never directly converted into cartilage-cells.

Towards the end of the embryonic period of life cartilaginous rings begin to be developed also around the central parts of the nervous system lying in the axis of the embryo. These rings, which become the vertebral arches, result from the transformation of the internal portions of the two oval masses situated one on each side of the groove or canal containing

* Histoire Naturelle des Poissons d'eau douce, par M. Agassiz, t. i. p. 98; and Entwickelungs-geschichte der Geburtshelferkröte, p. 47.

† Physiology, p. 1613.

the nervous centres. The remaining portions of the masses are converted into muscular tissue and integuments. The spinal chord also, as well as the chorda dorsalis, is provided with a kind of sheath, but not a fibrous one, such as is possessed by the latter structure.

*Development of the Vascular System.**

Formation of the Heart.—The account given by Reichert † of the mode of development of the heart in frogs, has been, for the most part, confirmed by the investigations of Vogt ‡ on the development of the toad, and those of Kölliker § on the development of the Batrachians generally. An almost similar mode of development is observed also in fishes, as shewn by the researches of Vogt on the development of the young salmon.‖ According to each of these observers, the heart, in its earliest formation, is composed of a solid compact mass of embryonic cells, similar to those of which the other organs of the body are constituted. It is at first unprovided with a cavity: but this shortly makes its appearance, resulting apparently from the separation from each other of the cells of the central portion. A liquid is now formed in the still closed cavity, and the central cells may be seen floating within it. These contents of the cavity are soon observed to be propelled to and fro with a tolerable degree of regularity, owing to the commencing pulsations of the heart.

These pulsations, according to Vogt, take place even before the appearance of a cavity, and immediately after the first "laying down" of the cells from which the heart is formed. Vogt has observed this especially in the embryonic salmon.¶ At first the contractions seldom exceed from fifteen to eighteen in the minute. In the production of them, the whole mass of cells appears to be concerned, for in none of the individual cells is there ever observed either contraction or enlargement during the pulsations: although M. Dumesny** states, as the result of observations on the embryos of Pæcilia Surinami, that such contractions and dilatations of the several cells may be distinctly observed. The occurrence of contractions of the walls of the heart previous to the formation of any muscular or other contractile tissue has been observed also in the chick by MM. Prevost and Lebert.††

Probably by the metamorphosis of the contained cells, the fluid within the cavity of the heart shortly assumes the characters of blood. At the same

* Müller's Physiology, p. 1620. † Müller's Physiology, p. 1526.

‡ Entwickelungs-geschichte der Geburtshelferkröte, p. 69.

§ An. des Sc. Nat. 1846, Zoologie, p. 96.

‖ Hist. Nat. des Poiss. d'eau douce, par M. Agassiz, tome i. 1842, p. 181.

¶ Op. cit. p. 182. ** An. des Sc. Nat. 1844, p. 344.

†† Ibid. 1844, p. 302. A long account of the mode of development of the heart, and of the subsequent changes in its form, and in the relations of its several parts is contained in this memoir.

time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its walls are composed are transformed into fibrous and muscular tissues, and into epithelium.

The development of the heart out of a solid mass of embryonic cells, and the early appearance of pulsations, has been described as occurring in Mammalia also, by Bischoff.*

The transformation subsequently undergone by the heart of the Mammalian embryo, and the mode in which its cavity is divided into its four compartments are described by Bischoff much in the same manner as they were by Rathke, Wagner, Meckel,† and others. (See fig. 19.) In his description also of the formation of the branchial arches and the arrangement of the first divisions of the aorta in the mammalian embryo, Bischoff agrees in all essential points with the accounts furnished by Von Baer,‡ and other observers (see fig. 20), and with the more recent extended observations of H. Rathke.§

Fig. 19.‖

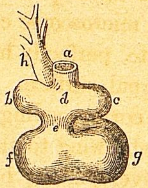
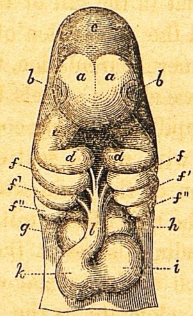


Fig. 20.¶



Development of Veins.—According to some recent researches by Professor Müller,** the posterior subvertebral veins, generally known as the vena azygos, and vena hemiazygos,†† are the true analogues of the cardinal

* Entwickelungs-gesch. der Säugeth. und des Menschen, p. 236.

† Müller's Physiology, p. 1621. ‡ Ibid. p. 1624. § Müller's Archiv. 1843.

‖ Fig. 19. A posterior view of the heart of an embryo dog, representing the early division of this organ into its several cavities. *a*, the common venous trunk cut across ; *b*, the left, *c*, the right auricular appendage ; *d*, middle space between the two future auricles ; *e*, canalis auricularis ; *f*, the left, *g*, the right ventricle ; *h*, trunk of the aorta with its first branches. After Bischoff. (Entwickelungs-geschichte des Hunde-Eies.)

¶ Fig. 20. Embryo dog representing the visceral or branchial arches. *a* and *c*, the brain ; *b*, rudimentary eyes ; *d*, first visceral arch ; *e*, continuation of the same : *f*, *f'*, *f''*, second, third, and fourth visceral arches; *g*, the right, *h*, the left auricular appendage of the heart ; *i*, the left, *k*, the right ventricle ; *l*, trunk of the aorta with its first branches forming the aortic arches. After Bischoff. Ibid.

** Vergleichende Anatomie der Myxinoiden, dritte Fortsetzung. Berlin, 1840.

†† Physiology, p. 1625.

veins of Rathke, which are persistent in fishes. The union of these two conjugate subvertebral veins in the human subject, and the subsequent termination of the true vena azygos, thus formed, in the vena cava superior, is little more than a repetition of what occurs in the Myxionoid fishes, where the symmetry of the venous system observed in fishes generally is destroyed; the union of the anterior and posterior subvertebral trunks (the jugular and cardinal veins of Rathke) taking place on one side only, and the two posterior veins uniting before joining the single anterior trunks.

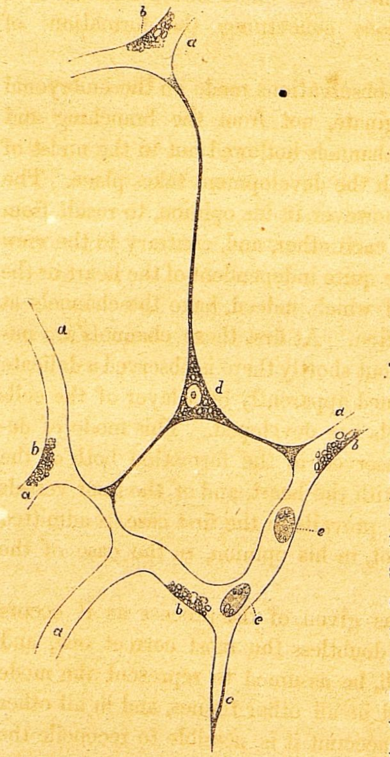
Development of Blood-vessels generally.—From his researches on the mode of development of the tissues in young Batrachians, Kölliker * has obtained some important results in relation to the formation of blood-vessels, which are especially valuable since they tend, in great measure, to reconcile the opposite opinions of those physiologists who adopt Schwann's view † in its fullest extent, by attributing the formation of blood-vessels exclusively to the direct transformation of nucleated cells, and of those who, with Plattner and others, consider that new blood-vessels are never formed except as off-shoots from previously existing vessels. Kölliker finds, that in the tail of tadpoles it is by the combined metamorphosis of cells and the production of off-shoots from tubes already in connexion with the general circulation, that new vessels are developed. In the tails of these larvæ all the vessels have originally the microscopic characters of the finest capillaries, being composed of a delicate, perfectly homogeneous membrane, with nuclei scattered along its internal surface. The mode of formation of the main arterial trunk and its corresponding vein, which run along the axis of the tail, cannot be observed, owing to the opacity of the surrounding tissues at the period of their development; but these two trunks, which at their distal extremity communicate with each other by a simple arch, elongate, as the tail increases in length, by pushing forth off-shoots which join and coalesce with embryonic cells situated around the posterior extremity of the chorda dorsalis. The first lateral vessels of the tail have the form of simple arches, passing from the artery to the vein, and are produced by the junction of prolongations sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed, and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches. In this manner the capillary net-work extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations by which the vessels communicate with the star-shaped cells, consist at first of narrow pointed projections from the side of a vessel, which gradually elongate until they come in contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril of fibrous

* An. des Sc. Nat. Août, 1846.

† See Müller's Physiology, pp. 404, and 1537.

tissue, and at first it is perfectly solid; but by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges, and a cavity then forms in its interior. Both the enlargement and hollowing out of the branch commence at the point of its departure from the vessel on the one hand, and at its point of junction with the cell on the other hand: the consequence of which is the appearance of great irregularity in the form and size of these various capillaries at their first formation. (See fig. 21.)* Of the star-shaped cells described by Schwann as being so numerous in the substance of the tail of young Batrachians, only a few are developed into blood-vessels, others are converted into lymphatic vessels, others into nerves, while many do not appear to undergo any metamorphosis.

Fig. 21.†



Plattner,‡ whose observations were made also on the tail of the tadpole, appears to have seen the formation of new vessels only as effected by the junction and coalescence of off-shoots from previously existing vessels. He observes that in this growing structure there may frequently be seen abrupt closed extremities of capillaries, and that sometimes long narrow processes may be noticed issuing from these extremities, and either gradually disappearing or seen uniting with other similar processes from neighbouring vessels, so that two such form by their union one arch which gradually enlarging and becoming permeable to blood corpuscles, constitutes a new capillary loop. A very similar account of the mode of production of new vessels in the tail of tritons and tadpoles is given also

* A very similar process to that above described is found by Kölliker to take place also in the development of the blood-vessels of the Sepia. Entwickelungs-geschichte der Cephalopoden, pp. 82-3.

† Fig. 21. Capillary blood-vessels of the tail of a young larval frog. Magnified 350 diams. After Kölliker. *a*, capillaries permeable to blood; *b*, fat granules attached to the wall of the vessels, and concealing the nuclei; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branching cell with nucleus and fat-granules; it communicates by three branches with prolongations of capillaries already formed; *e*, blood-corpuscles still containing granules of fat.

‡ Müller's Archiv, 1844.

by MM. Prevost and Lebert,* who, with Plattner, are of opinion that such vessels are always formed centrifugally, and under the influence of the circulation, by arches passing from a minute artery to a corresponding vein. These arches, they state, are formed in spaces left by the separation of the cells of the part in which the development of vessels takes place, and do not result as Schwann and Kölliker describe, from the coalescence of the branches proceeding from cells. The circumstance which, in their opinion, has led to the supposition of this latter being the true mode of formation, is the resemblance to cells presented by the interspaces themselves. From their observations on the development of the chick also,† Prevost and Lebert arrived at similar conclusions concerning the formation of blood-vessels.

In the opinion of Vogt also, from observations made on the embryonal salmon,‡ blood-vessels invariably originate, not from the branching and coalescence of cells, but as spaces or channels hollowed out in the midst of the cell-substance of the part in which the development takes place. The formation of these channels appears, however, in his opinion, to result from a simple separation of the cells from each other, and, contrary to the view of Plattner, Prevost, and Lebert, to be quite independent of the heart or the rest of the circulation, with neither of which, indeed, have the channels at their first formation, any communication. At first these channels are unprovided with distinct bounding walls, but shortly there is observed a delicate membranous lining to the canal, formed apparently by a layer of the cells in the midst of which the new vessels are developed. This mode of development, according to Vogt, is observed in the formation both of the first embryonic trunks in connection with the heart, and of the finer vessels or capillaries in other parts. That it prevails in the first case, is admitted also by Kölliker,§ but that it does not, in his opinion, in the case of the finer vessels, has been already shewn.

The description which Kölliker has given of the process as it occurs in the tail of young Batrachians, is doubtless the most correct one, and it may, with every probability of truth, be assumed to represent the mode in which blood-vessels are developed in all other tissues, and in all other classes of animals. With Kölliker's account it is possible to reconcile the descriptions furnished by Plattner and others, even though contrary to the designs of the authors; for with the exception of admitting the influence of cells, their account of the gradual formation of arches by the junction and coalescence of fine processes, and the gradual conversion of these into permeable tubes, closely accords with that given by Kölliker. The description furnished by Vogt is, however, so much opposed to that of Kölliker, that the difference must either be attributed to some misconception of

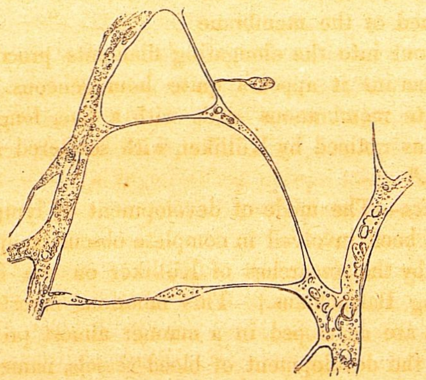
* Ann. des Scien. Nat. 1844, p. 222. † Ann. des Scien. Nat. 1844, p. 265.

‡ Hist. Nat. des Poissons, t. i. p. 206 ; and Entwickel. der Geburtshelferkröte, p. 71.

§ Henle and Pfeufers Zeitschrift für rationelle Medizin, 1845-6.

appearances by this usually most accurate observer, or, what is less probable, to the existence of another process less simple than the former, by which also the development of blood-vessels may be effected. Of the correctness of Kölliker's account, the writer can speak with complete certainty, from having, in some investigations with Mr. Paget, observed an almost exactly similar series of changes in the fine gelatinous tissue conveying the umbilical vessels of a sheep's embryo seven lines in length to the uterine cotyledons. Perhaps no better tissue than this could be selected for witnessing the mode of development of blood-vessels, for it is exceedingly fine, transparent, and composed almost entirely of a homogeneous substance, in which numerous scattered cytoblasts and cells, with developing blood-vessels, are almost the only objects seen. In some portions the development of vessels is complete, networks of various sized tubes filled with blood-corpuscles alone appearing. But in most other portions, together with completely formed and permeable vessels, the various steps in the development of these from elongating and branching cells, are distinctly seen. In such places are observed chains and networks of cell-like bodies, mostly filled with granular matter, and occasionally presenting a clear oval nucleus, and connected to each other by exceedingly slender filaments, some of which appear tubular, and in many instances are connected with blood-vessels of considerable size (see fig. 22). The cell-like bodies thus connected are of various shapes, most of them round or oval, many very narrow and spindle-shaped, some angular and elongated from their angles. The threads of connection are attached to the angles and points of the elongated bodies, and in the case of the round and oval ones, are so attached that these bodies appear like varicose or aneurismal enlargements.

Fig. 22.*

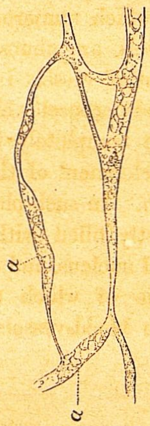


The various transitional states, from the fine solid threads of connection, to permeable tubules containing one or more rows of blood-corpuscles, are very manifest. As observed by Kölliker, the formation of a tubular cavity in the filaments appears, though not invariably, to commence at the points of their attachment to permeable blood-vessels and to the cell-like bodies. Occasionally blood-corpuscles may be traced

* This and the following figure, for the use of which the writer is indebted to the kindness of Mr. Paget, represent several of the appearances described in the text.

for a short distance down one such filament in connection with a vessel, and then observed to cease abruptly at a part where the filament becomes impermeable, and this apparently not from collapse of its walls, but either from no tubular cavity at all, or only an exceedingly narrow one, having yet been developed in its fine thread-like structure. In other instances isolated parts along the course of the fine filaments appear first to have become hollow, for here and there are observed isolated groups of coloured nucleated blood-corpuscles in distended parts of the narrowest tubes (*a a*, fig. 23). This circumstance would seem to prove that just as the heart and first blood-vessels are developed independently of each other, so may perfect blood-corpuscles be developed in parts not in immediate connection with the already formed vascular system, and from other materials than those derived directly from the contents of the blood-vessels; for in several of the instances in which the above peculiarity was observed, the part containing corpuscles was connected at either extremity with a blood-vessel or an elongated cell only by an exceedingly fine filament, which appeared quite incapable of transmitting a particle of even much less size than a blood-corpuscle. The walls of the fine tubes, as was observed by Kölliker, appear to be formed of the membrane of the cell which is drawn out into the elongating filaments proceeding from these bodies: in structure it appears quite homogeneous. The large vessels possess delicate membranous walls with a fine, longitudinally fibrous structure, and, as noticed by Kölliker, with scattered nuclei imbedded in their substance.*

Fig. 23.



Development of Lymphatics.—The mode of development of lymphatic vessels, which has hitherto been involved in complete obscurity, appears to be now fully elucidated by the researches of Kölliker on the formation of the tissues in young Batrachians.† This laborious investigator has found that these vessels are developed in a manner almost precisely similar to that pursued in the development of blood-vessels, namely, by the junction and fusion of processes from star-shaped cells with each other, or with off-shoots proceeding from already formed vessels. The chief point in which the development of lymphatics differs from that of blood-vessels, is in the processes from the cells, and from already formed vessels, uniting directly with each other, and thus producing a tube which does not give off lateral communications so as to form a network; for the

* The chief interest of the above observations is in their proving that the blood-vessels in Mammalia are developed after a plan exactly similar to that observed by Kölliker in Reptiles.

† An. des Sc. Nat. 1846, p. 99.

lymphatics, at their first formation, as in their perfect state, are distinguished from blood-vessels by the rarity of their anastomoses.

*Development of the Nervous System.**

First Traces of the Nervous System.—As was before observed (page 84) the account given by Reichert of the original formation of the central parts of the nervous system has been considerably modified by the investigations of Bischoff on the development of Mammalia.† The two oval masses or laminæ, between which the primitive groove is situated, are not, as was shewn also by Von Baer, the parts out of which the nervous system alone is formed, but are for the most part merely the foundations for the formation of the dorsal part of the trunk of the body, the central nervous system being developed only from that portion which immediately borders upon the primitive groove. Concerning the time at which this development first presents itself, Bischoff offers a somewhat different account to that given by Von Baer, who was of opinion that it did not commence until after the conversion of the groove into a canal by the junction of the lateral masses on each side of it. But Bischoff states that previous to the formation of a canal, nervous substance is developed along the whole inner surface of the groove, and apparently by a metamorphosis of the portions of the lateral masses immediately contiguous to the groove. The substance composing these portions gradually assumes a pellucid aspect like nervous substance, and increases in quantity : the inner border of each mass thus altered, then approximates and gradually unites with its fellow of the opposite side, so as to convert the previous groove into a tube, the walls of which thus consist of nerve-substance, while the hollow axis constitutes the central canal of the spinal cord. The approximation and union of the margins of the groove takes place first about the middle of the groove, and then proceeds upwards and downwards from this point. At the commencement of this union at the middle part of the groove, the upper or cephalic is formed (as was shewn also by Reichert in the chick)‡ into three successive dilatations which are the vesicles from which the brain is formed. At the opposite or caudal extremity the groove presents a lancet-shaped dilatation : this corresponds to the future Cauda equina (or Sinus rhomboidalis, as it is named in birds, *vide* fig. 11, p. 84). That the two oval masses bounding the primitive groove do not constitute the rudiments of the central parts of the nervous system, is shewn to be the case in Amphibia also, from the result of Vogt's investigations on the development of the toad.|| In this amphibious animal, he finds, as Bischoff has found in Mammalia, that the central nerve-substance is

* Müller's Physiology, p. 1627.

† Entwickelungs-gesch. der Säugeth. und des Menschen, p. 165, *et seq.*

‡ Müller's Physiology, p. 1547. || Entwickelungs-gesch. der Geburtshelferkröte, p. 66.

developed as a very thin layer which separates from the sides and bottom of the primitive groove; but contrary to Bischoff's observations, he states that the formation of nerve-substance does not take place until the primitive groove is converted into a canal by the junction of the margins of the lateral masses of cell-substance by which it is bounded.

Development of cerebral hemispheres.—It is stated by Professor Retzius* that the three portions of the cerebral hemispheres in the human embryo are developed, not at once, but at three separate periods. In the first of these periods, which extends from the second to the third month, the anterior lobes are formed; during the second period, which is comprised between the end of the third and the beginning of the fifth month, the middle lobes are formed; after this, therefore last of all, the posterior lobes are developed.

The inferior horns of the lateral ventricles and the hippocampi do not appear until the second period; at this period also the optic thalami make their appearance, and after these the tubercula quadrigemina.

Development of the Alimentary Canal.†

A somewhat different account of the mode of development of the Alimentary system of the toad to that given by Reichert‡ of the same process in the frog, has been furnished by Vogt.§ In the opinion of the former observer, the Alimentary canal is formed from the central cells of the yolk, but according to Vogt, it is formed from the internal or so called mucous layer of cells of which the germinal membrane or cortical part of the yolk is composed. On making a longitudinal section of the embryo and yolk through the chorda dorsalis, at the time of the formation of the branchial arches, the central part of the yolk (dotter-kern) is observed as a loose globule surrounded by a tolerably thick layer of cortical cell-substance. In the midst of this cortical layer the chorda is imbedded, being separated from the nucleus (or central part) of the yolk by a considerable quantity of the cells. In front, immediately beneath the elongated cephalic portion of the axis, there is observed a slight depression, which is the rudiment of the cavity of the mouth. At this time no separation of the cortical layer of cells into serous and mucous laminæ has taken place. As the growth of the branchial arches developed from the undivided cortical layer proceeds, the portion of the yolk-nucleus corresponding to the rudimentary mouth becomes depressed. The division of the germinal membrane into its serous and mucous layers now gradually commences. The latter separates itself from the former over its whole extent, except at the part corresponding to the rudimentary

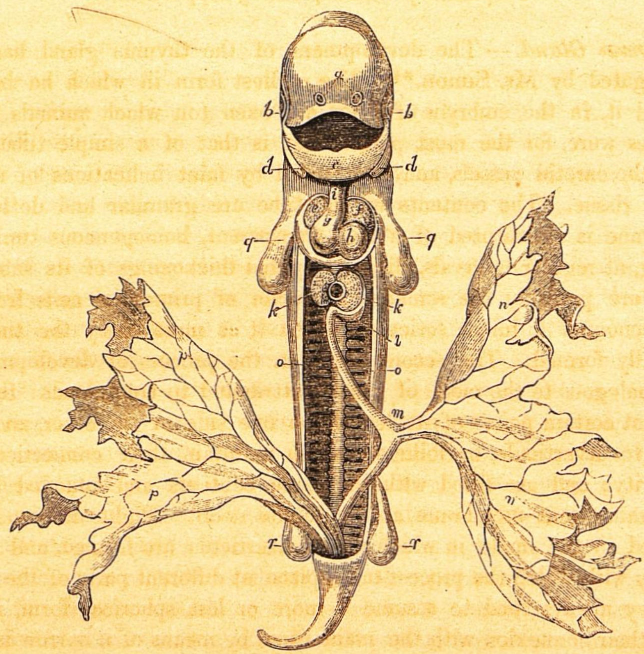
* Arch. d'Anat. Gen. et de Phys. Janvier, 1846, p. 24.

† Müller's Physiology, page 1633. ‡ Ibid. p. 1527.

§ Entwickelungs-ges. der Geburtshelferkröte, p. 67.

mouth, that corresponding to the anus, and along the entire vertebral line. While this separation is taking place, masses of cells from the mucous layer are left between the two laminæ; from these the liver and the Wolffian bodies are formed. When thus separated from the serous layer, the mucous layer forms a completely closed sac containing the yolk-nucleus. Shortly, over its whole external surface, there is developed a fine layer of cells, which at the above-mentioned points of attachment, becomes continuous with a similar layer of cells simultaneously developed along the inner surface of the serous lamina; and from these united layers of cells are subsequently formed the peritoneal sac and the mesentery. By the absorption of the membranes at the points corresponding to the cavity of the mouth and the anus, the sac formed by the mucous layer is opened, and the character of the Alimentary canal is thus assumed by it. During the subsequent growth of the intestine the

*Fig. 24.**



* Fig. 24. An embryo dog representing the junction of the umbilical vesicle with the intestinal canal. *a*, rudimentary nostrils; *b*, rudimentary eyes; *c*, the first visceral arch; *d*, the second visceral arch; *e*, the right, *f*, the left auricular appendage; *g*, the right, *h*, the left ventricle of the heart; *i*, the aorta; *k*, the liver, between the two lobes of which is perceived the divided orifice of the omphalo-mesenteric vein; *l*, the stomach; *m*, the intestine, communicating with the umbilical vesicle *n*; *o*, the Wolffian bodies; *p*, the allantois; *q*, the upper extremities; *r*, the lower extremities. After Bischoff. (Entwick. des Hunde-eies.)

central yolk-cells, which lie free in the cavity, and are not attached to its internal surface, gradually, and at length completely, disappear. They are not directly converted into the cells of the mucous membrane of the intestine.

With regard to the first formation, and subsequent development of the intestinal system in Mammalia, the account given by Bischoff is in close accordance with that furnished by Von Baer.* (See fig. 24.) The process pursued is very similar to that which takes place in the development of the intestine in the chick.†

Digestive Glands.—The account given by Professor Müller‡ of the mode of development of the large glands opening into the intestinal canal, as the liver and pancreas in birds, has been for the most part confirmed by Bischoff, in the case of Mammalia.§ The salivary glands also pursue a similar mode of development.||

Development of the Respiratory Apparatus.¶

Thymus Gland. — The development of the thymus gland has been investigated by Mr. Simon.** The earliest form in which he has discovered it, in the embryos of swine and oxen (on which animals his researches were, for the most part, made), is that of a simple tube, lying along the carotid vessels, and surrounded by faint indications of nascent areolar tissue. The contents of the tube are granular and dotted; its membrane is constituted of a fine, transparent, homogeneous tunic, presenting, at regular intervals, slight elongated thickenings of its substance, which are probably the remains of nuclei of primordial cells from the coalescence of a linear series of which it is most likely the tubule is originally formed. The second stage in the process of development is very analogous to the mode of growth attributed to true glands: the tube bulges at certain points of its length on one side or the other, and gives origin to diverticula or follicles, which maintain their connection with its cavity; and are filled with the same contents and bounded by the same transparent membrane as the tubule itself. Slight differences are observed in the mode in which these diverticula are formed, and in the rapidity with which the process takes place at different parts of the gland, but they always tend to assume a more or less spherical form, and to retain their connexion with the main canal by means of a narrow isthmus of communication. In the further growth of the gland secondary and tertiary hollow projections extend from each of the primary follicles, and by a continuation of the process, new groups of follicles are successively

* Müller's Physiology, p. 1568, and fig. 208. † Ibid. p. 1540.
‡ Physiology, vol. i. p. 489. § Op. cit. p. 322. || Page 323.
¶ Müller's Physiology, p. 1634.
** A Physiological Essay on the Thymus Gland. London, 1845, 4to.

formed, and, thus the gland attains the size and apparently complex structure which distinguish it in the mature fœtus. Each of the new follicular or vesicular off-shoots, maintain, like the first, a free communication with the primary tube, although in the fully-developed glands this is difficult to be shewn.

*Development of the Wolffian Bodies, Urinary Apparatus, and Sexual Organs.**

Wolffian Bodies.—In his account of the development and relations of the Wolffian bodies in Mammalia, Bischoff,† for the most part, agrees with Professor Müller ‡ in his description of these bodies, though in some particulars he differs from him. Like Müller and Von Baer, he describes the corpora Wolffiana as double organs from their first formation, and states that he has examined them in several Mammalian embryos, at an age at which they could be perceived only with the microscope, but that they never appeared to proceed from an originally single organ, as is said by Rathke to be the case in birds.§

Although Bischoff is opposed to Reichert's view,|| that the allantois is developed from the corpora Wolffiana,—having shewn, as already observed (page 86), that, in all the Mammalian embryoes which he had examined for the purpose, the development of the allantois takes place before any trace of the Wolffian bodies can be perceived—yet he maintains, as has been since done by Langenbeck (page 88), that when these bodies are formed, their excretory ducts communicate directly with the allantois. Indeed, this view is now admitted by most physiologists.

According to Professor Müller,¶ the excretory duct of each Wolffian body in Mammalia proceeds from the lower extremity of the organ instead of running along its outer side as is the case in birds: the filament along the outer side of the Mammalian Wolffian body which appears to correspond to this excretory duct in birds, being, in Professor Müller's opinion, the Fallopian tube in the female, the vas deferens in the male. Bischoff, however, agrees with Oken and Himly that this latter filament contains in Mammalia as well as in birds, the true excretory duct of the Wolffian body; having injected the organ through the duct in this filament, and having also succeeded in forcing by compression the contents of the organ into it. As well as containing the excretory duct of the Wolffian body, however, this filament also contains (as Müller said) the tube which passes to the rudimentary testis or ovary, and which in the male becomes the Vas deferens, in the female the Fallopian tube.**

* Müller's Physiology, p. 1635.

† Entwickelungs-gesch. der Säugeth. und des Menschen, p. 340–9.

‡ Physiology, pp. 1635-40.

§ Beiträge zur Geschichte des Thierwelt. t. iii. p. 50.

|| Müller's Physiology, p. 1554.

¶ Physiology, p. 1637.

** Bischoff, op. cit. p. 371.

Concerning the use of the corpora Wolffiana no doubt now exists of their being organs for the elimination of the urinary secretion during the early periods of embryonic life, and thus temporarily discharging the functions of the kidneys, which are not developed until a later period. Bischoff has detailed all the conclusive evidence in favour of this view.

Dr. G. L. Kobelt has recently published an essay,* the chief object of which is to shew, that, contrary to the opinion of Professor Müller,† and most other physiologists, the Wolffian bodies do not in either sex disappear during, or after, intra-uterine life, but that in the male sex most of the middle tubes of each Wolffian body become joined to the coni vasculosi of the testicle and so constitute the epididymis, while in the female sex also these bodies persist during life in the form of a structure closely analogous to the epididymis, and attached to the ovary.

Ovaries and Testes.—Bischoff‡ observes, that in Mammalian embryoes the ovaries and testes do not appear until some time after the formation of the other chief organs, and after the Wolffian bodies have made considerable progress in their development. They make their appearance, however, before the kidneys. As remarked, also, by Valentin, no difference in structure can be discerned between the testes and ovaries at their first formation. According to Valentin's account of the formation of the tissue of the testis,§ the first traces of the tubuli seminiferi appear in the form of transverse lines or streaks on the surface of the organ. These divide into narrower striæ which are subsequently converted into the seminiferous tubules. Bischoff,|| however, is opposed to this view of the development of the seminiferous tubules, and is of opinion that they are formed from nucleated cells which arrange themselves in linear series, and become fused at their opposed surfaces, in a manner similar to that which he considers to be pursued in the formation of the uriniferous tubules of the kidney.¶ For Valentin's account of the formation of the tissue of the ovary, and for Bischoff's opinion of this account, see page 36.

Rudimentary Uterus in the Male.—In the account given by Professor Müller ** of the mode in which the sinus urogenitalis of the early embryo is subsequently divided into two portions, pars urinaria, and pars genitalis, it is stated that while the former is converted into the urinary bladder the latter is transformed into the vesiculæ seminales in the male, and into the uterus in the female. In relation to this subject an interesting fact has been discovered by Professor E. H. Weber,†† namely, that in the males of several mammiferous animals which he examined, and in man, the organ analogous to the female uterus which is formed in

* Der Neben-Eierstock des Weibes, &c. Heidelberg, 1847. † Physiology, p. 1637.
‡ Entwickelungs-gesch. des Säugeth. und des Menschen, p. 355.
§ Entwickelungs-geschichte, p. 391. || Op. cit. p. 357. ¶ Page 354.
** Physiology, p. 1639.
†† Zusätze zur Lehre Vom Baue und Verricht. der Geschlechts-organe, p. 11.

the embryo, persists in a more or less developed state, throughout the whole of adult life. In man this rudimentary uterus exists in the form of a somewhat oval vesicular body imbedded in the substance of the prostate gland: a portion of it projects as a narrow ridge along the middle of the lower surface of the prostatic portion of the urethra, and is commonly known as the *caput gallinaginis* or *verumontanum*. That it is a hollow body, and has no communication with the prostate, may be shewn by inflating it with air. Very commonly the orifice of this, which Weber calls the male uterus, remains patent and may be discerned on the middle line of the urethra between the openings of the two ejaculatory ducts; sometimes it is very narrow, and in a few cases is even entirely closed. The male uterus is still more manifest in the beaver, where it is found enclosed within a fold of the peritoneum, and situated between the urinary bladder and the rectum, exactly in the position occupied by the uterus in the female beaver: in the male, also, as in the female, this organ is two-horned. Likewise in the male rabbit a rudimentary uterus exists and occupies the same situation as the fully developed organ of the female.* The Vasa deferentia open into the lower part of this male organ just as their analogues the Fallopian tubes open into the upper part of the female uterus. It has also been found by Weber that the walls of this rudimentary uterus possess distinct muscular fibres, and moreover that when mechanically or electrically irritated they contract and manifest distinct peristaltic movements.

In the newly-born rabbit, the organs of generation, both external and internal, so closely resemble each other in the two sexes, that it is only possible to distinguish the male from the female by the manner in which the Vasa deferentia differ from the Fallopian tubes. A male rudimentary uterus has also been found by Weber, in the dog, cat, sow, and horse. In the three former animals the orifice of the uterus usually appears closed: but in the horse, as in man, it is frequently found open.

The permanent existence of a rudimentary uterus in the male, accounts satisfactorily, in Weber's opinion, for the presence of a large uterus in the so-called male hermaphrodites of the human subject; such a uterus is of course only the vesicula prostatica, or rudimentary uterus, in a more fully developed state.

* Weber's observations have been confirmed by Huschke. Lehre von Eingeweid. des Menschl. p. 410.

DEVELOPMENT OF THE ANIMAL TISSUES.*

It is proposed in the following pages to offer some account of the present condition of the theory of cell-development, especially in relation to the following points:—

1. The nature and composition of the several parts of which a cell is constructed.

2. The order in which these several parts are developed in the formation of cells.

3. The manner in which the multiplication of cells is effected.

4. The transformations undergone by cells in the development of tissues.

1. Very little requires to be said concerning the *composition of the cell* itself. Its membrane or wall appears, by almost universal assent, to be formed of a protein-compound, most probably of albumen, except in a few cases in which it seems to be composed of a substance more allied to fibrine.† Although the cell-wall is rendered transparent and indistinct by acetic acid, yet it is not dissolved by this reagent, as is usually supposed to be the case, for on the addition of an alkali, such as a solution of potash or ammonia, its form and other external characters are in many cases restored.‡ With respect to the *contents* of cells, it is perhaps sufficient to state that further investigations continue to shew how various these may be, the varieties being as numerous as the functions which the cells discharge, and often differing in the same cell at different periods of its life. These contents, although occasionally composed of a clear fluid of various consistency and colour, are usually more or less granular, the granules consisting of different colouring matters, of fat particles, and of a fine molecular substance, whose nature is still obscure.

There is much discrepancy in the accounts given by different writers concerning the composition and general characters of the *nucleus*. This discrepancy is probably in great measure due to the fact, that after their formation the nuclei undergo various alterations in aspect if not in composition, and in some measure also to the fact of there probably being some original differences in the nuclei of different cells. Sometimes the nucleus occurs as a more or less solid body of a granular aspect, while at other times it appears as a pale vesicle with a distinct cell-wall and fluid contents. And between these two conditions varieties are occasionally found which would seem to prove that the one is only a modification of the other, and that these several varieties represent so many transitional stages between the two. The pale vesicular form is by far the most general one,

* Müller's Physiology, p. 1641.

† Kölliker, Entwickelungs-geschichte der Cephalopoden, p. 154.

‡ Donders, Holländische Beiträge zu den anat. und physiol. Wissenschaften, 1846.

and in Kölliker's opinion,* is the constant form of the nucleus in the early stages of the cell's life. It has been long known that the nucleus has a different composition to that of the cell, many agents which act upon the one having no effect upon the other. Kölliker† is of opinion that the membrane of the vesicular nucleus is composed of pyin, the clear contents of albumen, and the nucleolus of fat. His opinion that the membrane is composed of pyin, is derived chiefly from the fact of the nucleus being insoluble in acetic acid, a property which is possessed by no other nitrogenous compound except chondrine;‡ and this substance is soluble in the gastric fluid, while the nuclei are not, neither is pyin. The presence of albumen in the contents of the vesicular nuclei he thinks is proved by the contents of the germinal vesicle (which he considers to correspond to the so-called nucleus of other cells) being rendered granular by ether. The fatty nature of the nucleolus is indicated by its aspect, and by the presence of fat in parts composed chiefly of cells.

Schleiden§ described the nucleus in the cells of plants as being invariably situated within the substance of the cell-wall, which at that point divides into two laminæ, between which the nucleus is placed. In animals also the nucleus is commonly situated at the wall of the cell, sometimes apparently imbedded in its substance, but according to Schwann,|| most frequently attached to its inner surface, and never invested internally by a layer of the cell-wall as it is in plants, according to Schleiden. Henle¶ states that sometimes, as in pigment-cells and the cells of the crystalline lens, the nucleus is situated outside the cell-wall, which at that part presents a shallow depression to receive it; but Dr. Sharpey** is inclined to doubt the exterior position of the nucleus in these cases. Occasionally the nucleus is situated towards the centre of the cell,†† as is well shewn in the cells of cylinder-epithelium.‡‡ In such cases, however, the nucleus does not usually appear to lie free in the cavity of the cell, and to admit of being altered in position as the cell rolls over, but it seems to be quite fixed, and probably adheres to the internal surface of the cell-wall which, in cylindrical cells, closely surrounds it in one plane, and in flat cells is in contact with it at opposite sides. It was stated by Hewson,§§ however, that when the nucleated blood-corpuscles of fish or reptiles are swollen with water, and watched when rolling over, the nucleus may be distinctly seen to

* Entwickelungs-geschichte der Cephalopoden, p. 142.

† Op. cit. p. 144–5.

‡ And according to Kölliker, fibrine, but in this he is manifestly wrong.

§ Müller's Archiv. 1838, p. 148.

|| Microscopische Untersuchungen, p. 210.

¶ Allg. Anat. p. 192.

** Quain's Anatomy, Fifth edition, p. xliii.

†† In the case of vegetable cells, M. Mohl believes that the nucleus is invariably central at the earlier periods of the cell's life, and that its parietal position, when it occurs, is only a secondary state. (Botanische Zeitung, 1846; and Taylor's Scientific Memoirs, vol. xviii. 1846.)

‡‡ See Müller's Physiology, Second edition, p. 418, Fig. 36, B and C.

§§ Works, edited for the Sydenham Society by Mr. Gulliver, p. 222.

fall from side to side in each distended corpuscle; and Schultz * appears to have recently advanced a similar opinion. But Henle† remarks that he has never been able to witness this phenomenon, and he considers the nucleus of blood-corpuscles, as also those of mucus-corpuscles and epithelium-cells, to be attached to the inner surface of the cell-wall.

The nature and composition of the *nucleoli*, or nucleus-corpuscles, still remain obscure. Henle ‡ is doubtful whether what have been described as nucleoli may not be merely spaces in the interior of the nucleus. He thinks that this view of their nature is supported by the circumstance of no apparent chemical difference being perceived between them and the nuclei; agents which destroy the one, invariably destroying the other also. Vogt,§ although he admits the real existence of nucleoli, usually of a vesicular character, yet agrees with Henle in regarding them as unessential elements of a cell. He states that when they appear, it is only at a late period of the cell's life, and that shortly after their formation they usually assume a vesicular character, and as they enlarge are probably developed into cells at the expense of the nucleus which they gradually destroy. Kölliker,|| however, entertains an entirely different view of the nature and importance of the nucleoli. In his opinion, the nucleus ought to be regarded as a primary nucleated cell, and the structure usually called a primary cell as a secondary cell. In the formation of such primary cell (the nucleus of other writers) he believes that a round, dark, apparently homogeneous substance is first developed in the formative fluid. Around this body, which by him is regarded as the nucleus, by others as the nucleolus, the wall of the primary cell is gradually developed. Occasionally two, more rarely three, and still more rarely four, dark particles are found in a single primary cell (nucleus). Whatever may be the number, one at least is invariably found in every such cell up to a certain period of its growth. When single, the particle is situated on the wall of the cell; when there are several particles, they may occupy a similar situation, or be free in the cavity of the cell. Occasionally one or two particles apparently identical with these are found also among the contents of the secondary cells (or primary cells of other writers). They have all the appearance of being composed of oil or fat. Indeed, they appear to be identical with the elementary granules commonly found in the cytoblastema, and which Henle (as well as others) describe as minute vesicular-looking particles of fat. And it is difficult to determine in what respect they differ, and why Henle should discard the use of the term nucleoli; for, as will be presently shewn, he admits the importance of the elementary granules in the first formation of cells. Kölliker confirms Vogt's statement that the nucleoli are sometimes deve-

* Henle's Allg. Anat. p. 192. † L. c. ‡ Op. cit. p. 151.

§ Entwickelungs-geschichte der Geburtshelferkröte, p. 118.

|| Entwickelungs-geschichte der Cephalopoden, p. 149.

loped into vesicles, which then enlarge, apparently at the expense of the nucleus which disappears when these vesicles have attained a certain size, the vesicles themselves likewise disappearing soon afterwards. But in other cases, as will be presently shewn, the nucleolus, instead of disappearing, becomes constricted in the middle, and subsequently divided into two equal portions, around each of which a new cellular body or nucleus is then developed.* In all those cases, however, in which the nucleus or cell undergoes transformation into a higher tissue, the nucleolus disappears.† But this is certainly not invariably the case, for in the persistent nuclei of capillary blood-vessels, of the sarcolemma, and of several other tissues, a small dark particle, apparently identical with the nucleolus, may usually be observed.

2. In considering the various modes in which the *development of cells* in the formative fluid or cytoblastema is effected, it must be remarked, in the first place, that it appears immaterial to the process in what part the formative fluid is situated. The same succession of changes in the formation of cells seems to be pursued whether the process occurs in the cytoblastema of the early ovum, in the secondary cytoblastema from which the several embryonic tissues are produced, or in the organisable material effused from the blood-vessels into the interstices of the various parts of the growing or adult body. The fluid in each case appears to possess the same formative properties, and the chief or only difference observed in the process relates to the mode in which the cells are ultimately disposed of. In the increase, also, of cells, by endogenous multiplication, the formative fluid out of which the young cells grow, so far as concerns its power of producing new cells, appears to be essentially the same as the cytoblastema elsewhere: and the differences in the mode of growth are probably more apparent than real, the developing cells in the one case lying free in the interstices of parts, in the other case being enclosed within a membranous envelope or parent-cell.

In the opinion of Schwann the development of cells pursues an almost exactly similar course in every case; and he believes that the subsequent multiplication of animal cells, is usually effected by the same series of changes as are undergone in their original development, the endogenous mode of origin so common in vegetable structures being rarely pursued in animal tissues. But, as will be presently shewn, the result of more recent investigations have made it probable that this mode of origin, or rather of multiplication, is of more frequent occurrence than Schwann supposed. The plan of cell development recognised by Schwann, is detailed in Professor Müller's Elements of Physiology.‡ In addition to this, the ordinary mode of development, Schwann also suggested the probable occurrence of a variety, or modification of it in some cases. For having observed that occasionally the nucleus of a cell contained two nucleoli, he thought that

* Kölliker, op. cit. p. 150. † Op. cit. p. 151. ‡ Pp. 398 and 1641.

the circumstance might be explained by conceiving that two (or more) contiguous nucleoli, with their layer of granular deposit, had fused together before either of them had attained such a stage of development as singly to constitute a nucleus. And in those cases in which the nucleus of a cell appears to consist of two or more portions, he inferred that the component parts were so many nuclei which had been contiguous to each other, and fused together before the growth of the cell-wall around each had made much progress.

According to Henle* the formation of cells takes place in three different ways; in two of these (which appear to be only modifications of each other) the nucleus is developed first, while in the third it is not formed until after the cell, or even does not appear at all. In whichever of these ways the cells are developed, numerous spherical or oval fat-like particles first make their appearance in the cytoblastema or formative fluid. In one of the three modes of development, a layer of the dimly-granular material of the cytoblastema appears to deposit itself upon one of these fat-like particles, and thus to form a nucleus, upon which a cell-wall then grows, though, as will be noticed again presently, in a manner somewhat different from that pointed out by Schleiden and Schwann. In another mode, the nucleus is formed by the grouping together and coalescence of two, three, or even four of the elementary particles; a cell-wall is developed around this compound nucleus in the same manner as around the simple one. As the growth of the cell proceeds, the component particles of the nucleus become completely fused together, and a single smooth body eventually results. The compound nature of the nucleus of epithelial cells, and of pus-corpuscles after being acted upon by water or dilute acetic acid, is by Henle attributed to the fact of such cells being examined at an early period of their growth, and previous to the complete coalescence of the several particles composing the nucleus.† Henle believes that this mode of development prevails among most elementary cells of the animal body, and he refers, in illustration of it, to the corpuscles of mucus and pus,‡ to those of the lymph and chyle, and to the cells of most glandular structures. With regard to the mode of production of the cell-wall around the nucleus, Henle is of opinion, with other physiologists, that the several elementary granules are so many particles of fat, and that around each one, or a group of them (according as the nucleus happens to be simple or compound) a layer of the albuminous matter of the cytoblastema coagulates and forms a kind of film or coating, in accordance with the fact pointed out by Ascherson,§ that

* Allgemeine Anatomie, pp. 152—162.

† Kölliker, as will be presently mentioned, offers a different explanation of this appearance.

‡ Vogel also describes the development of pus in the same way. (Müller's Physiology, p. 466; and Pathologische Anatomie des menschlichen Körpers, 1845, p. 90.)

§ Müller's Archiv, 1840, Ueber die physiolog. Bedeutung der Fettstoffe, &c.

minute globules of oil when brought into contact with liquid albumen, become at once invested by a coherent layer of the albuminons substance, and thus acquire a vesicular character.

On comparing the above two modes of cell-development with the account furnished by Schwann, it will be observed that there is no striking difference between them; the first plan of development described by Henle agrees essentially with that stated by Schwann, while between Henle's second plan and Schwann's explanation of the origin of the cells containing two (or more) nucleoli, the difference is more apparent than real, and is not in either case founded on direct observation. The chief discrepancy in the accounts of these two observers, appears to consist first in Henle's disinclination to admit the existence and importance of nucleoli, though, as before observed, there is no good reason for regarding the nucleoli as structures dissimilar from Henle's elementary particles or granules; and secondly, in respect of the manner in whieh the cell-wall is developed around the nucleus.

In Henle's third mode of the development of cells, a large quantity of the elementary granules arrange themselves together into a more or less spherical mass, around which a delicate cell-wall is subsequently formed; but it is not until a later period, if at all, that a nucleus can be perceived in the midst of this mass. Illustrations of this mode of development are presented by the large granular bodies met with in the first milk or colostrum, by the so-called compound inflammation- or exudation-corpuscles, and by many of the globules found in malignant tumours and other morbid products.*

* It should be remarked, however, that doubts are entertained by several physiologists, of the above being the mode in which the granular exudation-corpuscles found in the products of inflammation, or in other diseased structures, are developed. Vogel (Pathologische Anatomie des menschlichen Körpers, p. 127) is of opinion that these corpuscles are cells which have an origin exactly similar to that described by Schwann, as occurring in the development of other nucleated cells; and he believes that they only subsequently assume the granular condition. Reinhardt (Archiv für pathologische Anatomie und Physiologie, by H. Virchow and B. Reinhardt, 1847,) entertains an almost exactly similar view, and he believes that the exceedingly granular condition of exudation-corpuscles and of other granular-looking cells, is probably always a later change due to the formation of granules of fat, and just precedes the cessation of their period of life, which event is manifested by the disappearance of the nucleus and cell wall, and by the breaking up of the cell into an irregular heap of granules. He believes also, that these retrograde changes take place in cells developed under normal as well as abnormal conditions, and he furnishes many examples in proof of this. The best of these examples is afforded by the changes which ensue in the cells composing the membrana granulosa of the Graafian follicle during the degeneration which the follicle undergoes in the ovary. These cells, in the mature Graafian follicle, are nucleated, and filled with tolerably clear albuminous contents; but as the follicle degenerates or retrogrades, the cells become opake from the formation of granules or particles of fat among their contents, the nucleus disappears, and ultimately the more or less thick yellowish substance filling the follicle, is found to consist almost entirely of granule cells (like exudation-corpuscles) and heaps of granules, into which the cells have broken up. On the other

Besides these three modes of cell-development, however, Henle recognises, with Schwann and other physiologists, another plan in which simple cells are developed, independent of a pre-existing nucleus; examples of this are seen in the chorda dorsalis of fish and reptiles, as Schwann pointed out, and in cryptogamic and many higher plants, in which a single minute spherule first appears, and this soon becomes a distinct vesicle, rapidly grows, and is eventually extended into a cell.

The results of investigations by Vogt,* on the development of fishes and reptiles, also tend to shew the occurrence of at least three distinct forms in which the development of cells may take place. In one of these forms the cells appear to owe their origin to a pre-existing nucleus, but in the two others they appear to originate independently of a nucleus.

As already stated, Vogt entirely agrees with Henle in his view of the unimportance of the nucleolus in the process of cell-formation. In by far the majority of cells in young Batrachians and fishes nucleoli were entirely absent; and in the few in which they existed, as the cartilage-cells of Batrachians, and the embryonic-cells of the salmon, they appeared to be structures of later formation, occurring as simple vesicles which gradually enlarged into cells apparently at the expense of the nucleus, which by degrees entirely disappeared. In no case did they appear to constitute the first stage in the development of cells out of the cytoblastema in the manner described by Schleiden and Schwann. The *nucleus,* however, appears to be an almost invariable constituent of the cell at whatever period of its life it be examined. But the relation, in point of time, which its development bears to the development of the cell, was found by Vogt, as by Henle and others, to vary in different cases. In one form of cell-development, namely, the production of the cortical cells of the yolk in the toad, the nucleus precedes, and evidently gives rise to, the formation of the cell. In another form, which, as shewn by Henle, is well illustrated in the chorda dorsalis of fish, the cells originate without the intervention of nuclei, which only make their appearance after the cells are fully formed. In the third form, the cell and its nucleus seem to be

hand, Bruch (Henle and Pfeufer's Zeitschrift, b. iv. p. 50) appears to agree with Henle, for he states that the large granular corpuscles frequently met with in cancerous growths, are formed by an aggregation of granules, within which a nucleus is shortly formed, and the whole then becomes surrounded by a cell-wall. Luschka (Entwickelungs-geschichte der Formbestandtheile des Eiters und der Granulationen. Freiburg. 1845.) also agrees with Henle, in believing that the exudation-corpuscles in inflammatory products are formed by the grouping together of numerous minute granules, around each heap of which a cell-wall is then developed, while a nucleus shortly afterwards makes its appearance in the midst. But he also believes that the corpuscles thus formed constitute only an early stage in the development of pus-corpuscles, into which they are afterwards changed by the absorption of some of their granular matter, and consequent diminution in size.

* Entwickelungs-geschichte der Geburtshelferkröte, 1842, pp. 118—27.

developed coincidently. For, in the embryonic cartilage of the toad, in which this mode of development occurs, Vogt never could detect either free nuclei or cells unprovided with nuclei; when nuclei were found, they were invariably surrounded by a cell-wall, and when cells were found, they invariably enclosed a nucleus. In explanation of this coincident formation of cell-wall and nucleus, Vogt suggests that probably one portion of the granular matter of the cytoblastema, from which a cell is about to be developed, may collect, centripetally, at the centre, to form a nucleus, while another portion may collect around, at some distance from it, by a centrifugal influence, and there form a cell-wall.

Kölliker's* opinion of the mode of origin of cells, founded upon the results of researches on the development of invertebrate animals, differs in several respects from those entertained by Henle and Vogt. For he believes that the so-called primary cell is, as Schleiden and Schwann described, in almost all cases developed around a nucleus, which persists for a greater or less length of time, and that the nucleus also is in most cases formed around a nucleolus. The irregular appearance frequently presented by the nucleus of pus-corpuscles, especially after being acted upon by dilute acetic acid, is not, as Henle supposed, an early character, and an indication of its being originally composed of two or more separate particles—for, at its first formation, the nucleus is invariably a simple vesicular body—but is an after effect, and is due to the nucleus being divided into two or more new vesicular bodies, each of which may, if carefully examined, be seen to contain a minute particle or nucleolus; and these, he thinks, originate by endogenous multiplication.

In a recent essay, H. Müller † has advanced an opinion concerning the development of the corpuscles of pus and of chyle, which differs from that of other writers, and from which it would seem that these corpuscles originate in a manner somewhat similar to the third mode of development described by Vogt. He believes that previous to the development of cells the chyle consists of a number of particles, some of which are soluble, others insoluble. In the production of chyle-corpuscles or cells, a number of both kinds of particles become aggregated into a mass; shortly after the formation of which, the insoluble particles collect together in the centre to form the nucleus, while the soluble ones dispose themselves around the circumference, and are transformed into the cell-wall. A very similar process he states to be pursued in the formation of pus-corpuscles.

Such are some of the principal observations which have been lately made on the subject of the development of cells. The amount might have been considerably extended by including the remarks of many other

* Entwickelungs-geschichte der Cephalopoden, 1844, p. 142.

† Beiträge zur Morphologie des Chylus und Eiters, in Henle und Pfeufer's Zeitschrift, b. iii.

writers on the subject, but since these have, for the most part, a tendency to confirm one or other of the views stated above, it is perhaps unnecessary to do more than refer to them here.* In collecting together the above facts, it has been the writer's endeavour to ascertain whether the various accounts of different observers could be so far reconciled as to furnish conclusions pointing to the existence of any one uniform and constant plan, according to which the development of cells is in all cases effected. But it will be at once evident, from what has been stated above, that so far as our present data extend, no such single uniform plan can be said to exist; though it is not improbable that further investigations will shortly lead to its discovery, and that then the several varieties hitherto observed, may be found to be only modifications of one universal mode of development.

From what has been said above, it appears tolerably certain that cells may sometimes originate independent of pre-existing nuclei, and that, therefore, the views of Schleiden and Schwann in respect of the importance of these structures in the genesis of cells, must be somewhat modified. Yet it is not satisfactorily shewn that in any mode of cell-formation cases ever occur in which one or more minute elementary particles, corresponding to the nucleoli of Schwann, do not exist previous to the formation of any other part of the cell. If subsequent investigations prove that the pre-existence of such particles is a circumstance of invariable occurrence, it may be reasonably inferred that they are the real germs or cytoblasts from which the cells originate. When once formed, these particles may give rise to the production of cells in one or other of the various ways above described. Each one may either grow and be itself developed into a cell by incorporating nutritive matter, and simply enlarging, as is supposed by Mr. Macleod † to be the case in the development of the blood-corpuscles of the chick, by Vogt ‡ in the development of the cells of the chorda dorsalis, and by Karsten § in the development of all varieties of cells. Or it may serve as a centre around which matter is deposited to form a nucleus, from which a cell-membrane subsequently springs in the manner maintained by Schleiden and Schwann to prevail in most vegetable and animal tissues. Or, again, it may serve as the true nucleus to a primary cell growing around it; and this, by Kölliker, is considered to be its ordinary office. It must be mentioned, also, that even a primary cell may act the part of a nucleus, so far, at least, as to cause the growth around it of another secondary cell-membrane.

* The whole subject will be found well discussed by Reichert, in his Reports in Müller's Archiv. during the last three or four years, by Kölliker in Schleiden and Naegeli's Zeitschrift, and by Henle in his late Reports in Canstatt's Jahresbericht.

† London and Edinburgh Monthly Journal of Medical Science, Sept. 1842.

‡ Entwickelungs-geschichte der Geburtshelferkröte, p. 126.

§ De Cellâ Vitali. Berlin, 1843.

Examples of this are furnished by the ganglion-corpuscles of nerve-substance, and by the ovum. Kölliker, indeed, considers that all ordinary nucleated cells should be regarded in the light of secondary or complex cells.

3. From the several details which have just been considered in relation to the development of cells, it would appear that in the cytoblastema there resides some power by which fresh cells can be continually formed out of an apparently homogeneous fluid. In order that this continual formation of successive crops of cells may be effected, it is essential, however, that constant supplies of new formative fluid should be provided, and it appears to be one of the purposes served by cells, to elaborate this fresh formative material, which, when perfected, is discharged by the solution of the membranous cell-walls. Out of the fresh cytoblastema thus prepared and liberated, the new cells are developed in one or other of the ways above pointed out. And it would seem, as stated by Schwann, that, in the case of animal structures, the continued increase of cells, is in most cases, effected by such fresh development in the free formative fluid. But in several other cases new cells are formed within the cells of a preceding generation, and by these they are surrounded until they have attained a certain degree of development, when they escape, apparently by rupturing the parent cell which then disappears. This *endogenous* mode of cell-formation, (or *multiplication*, as it is commonly termed,) although of common occurrence among vegetable structures, is, however, comparatively rare in animals; the ovum, cartilage, and a few other structures presenting the only known examples of it. It differs from the original development of cells in the circumstance of the new cells being produced more or less directly from some part of a pre-existing cell, which thus acts as a kind of re-productive organ. But it is not improbable that the difference is one more apparent than real, and consists simply in the circumstance of the source whence the new cells originate, being in the one case retained within the parent-cell, and in the other case set free.

The best examples of the endogenous mode of cell-multiplication have been already mentioned in describing the changes which ensue in the development of the ovum.* It was there shewn (in the case of the ovum of Cucullanus elegans) that according to Kölliker's observation the first step in the process of multiplication consists in the nucleus of the first cell which is formed after the disappearance of the germinal vesicle, becoming constricted in the middle, and subsequently dividing into two equal halves, each of which serves as a separate nucleus, around which a new cell forms; and each new cell in its turn gives rise to two others formed in the same way, and so the process goes on until the whole mass of the ovum is made up of such cells. And Kölliker appears to be of opinion that in most other cases of cell-multiplication the division of the nucleus is the first essential step in the process.† Other cases, however, seem to occur

* See especially p. 66 and p. 71. † Entwickelungs-gesch. der Cephalopoden, p. 150.

in which the nucleus, instead of dividing into two portions, only breaks up into several particles (though even this may be effected by successive duplications) each of which appears to possess the power of enlarging and becoming vesicular; the several minute vesicles as they increase in size gradually obliterating the original nucleus, and eventually constituting the chief contents of the cell. Each of these minute vesicular particles probably constitutes a germ of a fresh cell, into which it is subsequently developed either by simple enlargement, or by serving as a cytoblast around which a cell-wall forms. In other cases, again, apparently under the influence of the nucleus when present, or even independent of it, minute vesicular bodies are developed within the cell itself, which by enlarging they gradually fill, and eventually burst. Previous to their discharge from the parent cell, or shortly afterwards, a new generation of cells is developed within each of them by the same process by which they themselves had been formed. Another form of cell-multiplication has been described as occurring in vegetable structures, in which a cell appears to divide by the formation of a partition across its cavity, whereby two new cells are formed. But as explained by Schleiden, in which explanation Dr. Sharpey* agrees, this apparent mode of division is probably merely an instance of the endogenous production of twin cells, the contiguous sides of which form the septum as in C, fig. 8, p. 71. In a few cases, again, the multiplication of cells takes place by the growth of young sprouts or offshoots from the parent cell. This variety, which is confined entirely to vegetable structures, is well illustrated in the mode of growth of the yeast-plant.†

4. The tendency of nearly all recent observations on the subject has been to confirm the general correctness of Schwann's account of the various *changes which the primary cells undergo in the production of the elementary tissues* of the body.‡ In some instances, however, there is sufficient evidence to shew that this account requires to be modified. This seems to be especially the case in regard to the cellular, tendinous, and elastic tissues, each of which was supposed by Schwann to be formed by the elongation of cells and their division into bundles of fibres. But that such a mode of development appears not to take place will be presently shewn when considering the transformations undergone by the nuclei.

In regard to the development of bone, a considerable amount of information has been of late added to the comparatively imperfect account of it furnished by Schwann. But it is considered unnecessary to enter here into the details of this, since the whole of the subject has been of late so ably discussed by Dr. Sharpey, in a standard work on anatomy.§

* Quain's Anatomy. Fifth edition, p. xlviii.

† For accounts of the above modes of cell-multiplication see especially Henle, Kölliker, Vogt, Reichert, and Vogel, in the works referred to.

‡ For this account see Müller's Physiology, pp. 397 and 1643.

§ Quain's Anatomy, by Dr. Sharpey and Mr. Quain, p. cxlvii.

Several new facts have also been added concerning the development of nerves, which tend to throw fresh light on the physiology of the nervous system, since they render it almost certain that the central terminations (or origin) of nerve-fibres are not disposed in loops, as until lately has been generally supposed to be the case, but that they pass directly into the nerve-corpuscles which compose so large a portion of the grey substance of nervous centres. Both Müller and Remak, several years ago, observed that from some of the corpuscles of the grey substance of the brain, spinal cord, and ganglia, fine tooth-like processes issue, and may be sometimes traced to the extent of many times the diameter of the corpuscles.* The resemblance which these processes bear to the delicate, grey filaments observed by Remak in the sympathetic nerves, led to the suggestion that the two are identical, and that the latter filaments take their origin directly from the ganglion corpuscles. These observations, however, do not appear to have attracted much further notice; but it has been found by more recent investigations, that Remak's suggestion concerning the origin of sympathetic nerve-fibres is perfectly correct, and moreover that the fibres of the cerebro-spinal nerves also have, as was indicated by Ehrenberg,† an exactly similar origin.‡ Without entering into the details of these important investigations, the consideration of which would be foreign to the present purpose, it may be remarked that in the junction of the nerve-fibres with the ganglion-corpuscles, the contents of the central part of the fibre (the axis-cylinder of Purkinje and Rosenthal, the primitive band of Remak) pass directly into the granular contents of the corpuscle, while the fine external sheath of the nerve-fibre becomes continuous with the membranous envelope, within which the granular substance of the corpuscle is contained. The phenomena observed during the development of nerve-fibres in the embryo, especially by Schaffner § and Kölliker,|| agree very closely with these facts. In the earliest period of its formation nerve-substance consists almost entirely of roundish, mostly nucleated cells filled with a finely granular material, and, with the exception of being somewhat smaller, exactly similar to the nerve-corpuscles found in the nervous centres of the adult animal. As the development proceeds, but previous to the appearance of distinct nerve-fibres, many of these cells send forth fine tubular processes of an apparently homogeneous structure, which unite with similar processes from other cells, and thus, in time, give rise to continuous nerve-tubules. Kölliker finds that in young

* Müller's Physiology, vol. i. p. 657. † Structur des Seelenorgans. Berlin, 1836.

‡ See Helmholtz, de Fabric. System. Nerv. evertebratorum. 1842; Kölliker, die Selbstand. und Abhang. des sympath. nervensyst. Zurich, 1844; Dr. Will, in Müller's Archiv. 1844; Dr. Todd and Mr. Bowman, Physiological Anatomy of Man, vol. i. p. 213; and more especially R. Wagner, Neue untersuchungen über den Bau und die endigung der Nerven und die Struktur der Ganglien, Leipzig, 1847, and Dr. F. H. Bidder, zur Lehre von dem Nervenfasern. Leipsig, 1847. § Schmidt's Jahrbücher, 1847.

|| An. des Sc. Nat. Zoologie, 1846, p. 104.

Batrachians, a complete network of nerve-tubes is formed by this junction and coalescence of the processes from branching cells: a similar observation was also made by Schwann.* According to Schaffner, as the nerve-tubules coalesce and increase in size, the walls of the cells from which they originate are gradually drawn out and merge into those of the tubules, while their granular contents also become continuous and identified with the contents of the tubules.

In considering the transformation which cells undergo in the development of tissues, too much stress cannot be laid on the importance of the share taken by the nuclei in these changes, especially since this appears to have been entirely overlooked by Schwann. It is proposed, therefore, to bring together some of the more striking circumstances which seem to demonstrate the importance of nuclei, whether considered as individual structures, or as component parts of cells. That the nuclei may exist in tissues apparently independent of cells, has been shewn especially by the observations of Mr. Paget,† who found that many morbid growths are composed almost entirely of corpuscles like nuclei or cytoblasts. These morbid structures were usually tumours of very rapid growth, and from the almost invariable presence of large quantities of nuclei, it would seem that they must play an important, if not the chief part in this growth. The abundance of nuclei in most, if not all, other actively growing tissues, healthy as well as morbid, their persistence in those tissues, such as the muscular, in which a constant waste and repair consequent on the active discharge of their function is taking place, their invariable existence in the secreting cells of all glands and epithelia, and their disappearance from the cells of fat, which when fully formed cease to perform any active function, all attest the importance of the share taken by the nuclei in the processes of growth, reproduction, and secretion. Equally strong confirmation of this is furnished also by the variety of examples in which development, in either structure or composition, is effected in the animal organism by cells unprovided with nuclei, while there are many instances in which nuclei, whether contained in cells or without them, appear to assume higher forms, or to be centres and sources of formative and reproductive power.‡ The evidence of these facts is based chiefly on his own observations on tumours above alluded to, and on the investigations of Professors Henle § and Goodsir,|| and of Mr. Simon.¶ The researches of the last-named observer on the glands without ducts, tend to prove the discharge of a large amount of gland-function by nuclei alone; for in the thymus, the splen, and other such glandular organs,

* Mikroscopische Untersuchungen, p. 177.

† Report on Anatomy and Physiology for 1844–5, p. 35.

‡ Mr. Paget, Lectures at the Royal College of Surgeons, May 1847. Lecture 5.

§ Allg. Anat. pp. 192—9.

|| Anatomical and Pathological Observations, 1845.

¶ A Physiological Essay on the Thymus Gland, 1845.

minute vesicular bodies, in all respects similar to nuclei or cytoblasts, exist in considerable abundance, and appear to be the essential parts concerned in discharging the functions of these organs. And Professor Goodsir's observations in several of his papers * seem to demonstrate the power of the nucleus both in the production and multiplication of cells, and in the formation and storing of secretions.

The transformation of nuclei into higher tissues has been shewn especially by the researches of Henle,† and more recently by those of Kölliker.‡ According to Schwann's system of cell-formation, the nucleus is supposed to disappear shortly after the perfect state of the cell is attained. But the results of recent observations have shewn that the disappearance of the nucleus is of much more rare occurrence than was supposed by Schwann to be the case, and, moreover, that instead of disappearing, the nucleus in many cases assumes a higher degree of development, and is transformed into a more or less persistent tissue. According to Henle,§ the only parts in which the nucleus disappears are the blood-corpuscles, the cells of the epidermis and the nails, and most of the fat-cells, the tubules of the crystalline lens and of enamel, and many of the cartilage-corpuscles. But in all fibres supposed to be formed from coalescing cells (except those of the lens and enamel), the nuclei remain, and, moreover, undergo remarkable transformations. For example, they assume an oval shape, then gradually elongating and becoming narrow, are converted into fine dark streaks, which lie in straight, angular, tortuous, or spiral lines upon the fibres. After being thus changed they either gradually disappear, or becoming more elongated and meeting with each other, they unite to form a new set of fibres, which, from their mode of origin, he calls nucleus-fibres. Occasionally these nucleus-fibres send off lateral branches, by which a kind of continuous network is formed over the surface of each layer of the tissue in which this arrangement occurs. Various other modes of arrangement of these nucleus-fibres are observed in different tissues. The fibres are remarkable for their dark well-defined outline, and being insoluble, like other nuclei, in acetic acid, their existence and peculiarity in a tissue may be at once ascertained by means of this re-agent. Ordinary elastic tissue appears, according to Henle,|| to be only a variety of such nucleus-fibres.

Another remarkable purpose served by nuclei in the formation of tissues has been pointed out by Henle as seen especially in the coats of blood-vessels. In the development of these coats, layer after layer of cytoblastema is deposited in the form of structureless membrane, and in each of these, nuclei are shortly formed and undergo several different changes. In the innermost layer cells grow around the nuclei, and thus is formed the

* Op. cit. articles "Centres of Nutrition," "Secreting Structures," and "Serous Membranes." † Allg. Anat. pp. 192—9. ‡ Entwickelungs-ges. der Cephalopoden, p. 145. § Allg. Anat. p. 192. || Allgemeine Anatomie, p. 407.

epithelial coat of the vessel. In the next layer, which forms the so-called internal coat of the vessel, the nuclei remain unaltered. But in the formation of the muscular or contractile coat of arteries, the nuclei elongate and arrange themselves in rows in the manner before described. Moreover each row of elongated nuclei appears to appropriate the adjoining strip of structureless membrane in which it is imbedded, and the result is that this membrane breaks up into a number of flat fibres, each bearing upon its surface the row of nuclei after which it was modelled. Organic muscular fibres of other parts of the body are formed after exactly the same plan. In the formation, also, of fibro-cellular or areolar tissue, the nuclei are arranged in rows, to each of which is appropriated a strip of the cytoblastema; and each such strip, instead of remaining flat and ribbon-like, as is the case in organic muscular fibre, breaks up into a bundle of parallel longitudinal fibrillæ. This is quite opposed to the account given by Schwann* of the development of fibro-cellular tissue. Kölliker,† in alluding to these several transformations undergone by the nuclei, mentions also, as other instances, the different modes of development of seminal filaments directly from nuclei,‡ and the growth of the spines of several invertebrate animals.

Arguments in favour of the view of the importance of the nuclei to the growth and well-being of the tissues in which they occur, are furnished also by the phenomena which attend their retrograde, as well as their advancing transformations—their degradation as well as their development. For it has been rendered highly probable by the investigations of Mr. Paget,§ that in all cases of atrophy accompanied with degeneration of tissue, the nuclei of the degenerated part lose their characteristic properties, or entirely disappear. This is especially the case in fatty degeneration (or atrophy) of muscle, of the liver and of the kidney, in all well-marked instances of which, the nuclei, of the fibres in one case, of the hepatic and renal cells in the other cases, have completely disappeared, their place being occupied with fat, in the form of granular matter, or drops of oil.

Development of the Blood.

It may be desirable here to present some account of the principal observations recently made on the development of the blood corpuscles. Concerning the original formation of these corpuscles in the embryo, the results of nearly all recent investigations tend to shew that, as was stated by Reichert,|| at the first appearance of a vascular system they consist, in all vertebrate animals, of nucleated, colourless, granulated cells, identi-

* Müller's Physiology, p. 1646, and fig. 253.

† Entwickelungs-gesch. der Cephalopoden, p. 145.

‡ For an account of these modes of development, see p. 41.

§ Lectures at the Royal College of Surgeons, May, 1847. Lecture V.

|| Müller's Physiology, p. 1550.

cal with the formative, vitelline, or embryonic cells of which all the structures of the embryo are originally composed; that they are, in fact, the central cells of the solid mass of which the heart and large blood-vessels at first consist. A difference of opinion, however, still exists with respect to the mode in which these original cells are converted into the characteristic corpuscles subsequently found in the blood.

According to Vogt, from observations made on the larva of the toad,† (Alytes obstetricans,) and on the embryo of the salmon (Coregonus palæa‡), the cell-wall of each original cell gradually disappears, and the liberated nucleus, in which a secondary nucleus is subsequently formed, becomes the true nucleated blood-corpuscle. The circumstances which he urges in favour of this view are, first, the close correspondence in size between the nuclei of the original cells and the true corpuscles of the blood; and, secondly, the non-existence of a nucleus at first in the small corpuscles, and its appearance subsequently. Against this view it is objected, by MM. Prevost and Lebert,§ from observations also made on Batrachians, that there is by no means so close a resemblance in size between the nuclei of the primitive cells and the corpuscles of the blood, as stated by Vogt, but that the size of the latter more nearly corresponds with that of the cells themselves: and that, contrary to Vogt's statement, a nucleus may be detected in the blood-corpuscle in all the phases of its evolution. According to these observers, the blood-corpuscles result from a direct transformation of the cells themselves, which assume an ellipsoid instead of their previously round form, become flattened, lose their granular matter, and acquire coloured contents. Kölliker, also, is opposed to the account given by Vogt, and is of opinion with Prevost and Lebert, that in Batrachians, and also in Mammalia, the embryonic cells themselves are directly transformed into the true blood-corpuscles. Like Prevost and Lebert, he also was unable to find non-nucleated corpuscles in the blood of larval frogs, and of the earliest embryos of Mammalia. A similar view to that of the last three named observers concerning the direct origin of the earliest blood-corpuscles from the embryonic cells, appears to be entertained also by most other physiologists.¶

The conversion of embryonic cells into true blood-corpuscles, in whatever way effected, is probably completed very shortly after the formation of a cavity in the heart and in the large blood-vessels in connection with

* Entwickelungs-geschichte der Gebürtshelferkröte, p. 70.

† In Agassiz's Hist. Nat. des Poissons d'eau douce, tome i. p. 203.

‡ An. des Sc. Nat. 1844, p. 212. § An des Sciences. Nat. 1846, p. 43.

‖ Mr. Macleod (London and Edinb. Monthly Journ. of Med. Sc. Sept. 1842,) is of opinion, however, that in the chick the earliest blood corpuscles are developed from minute dark spherical granules of which alone the blood at first is composed. He believes that each of these possesses the power of enlarging, and being developed into a circular nucleated cell, which subsequently flattens, assumes colouring matter, grows oval, and thus becomes a true red blood-corpuscle.

this organ, and after this period their share in the production of blood-corpuscles appears to cease. The next point, therefore, to be considered, is the mode in which the subsequent multiplication of the corpuscles thus formed is effected. According to Kölliker,* this multiplication in the earliest period of embryonic life takes place, in Mammalia, either by the actual division of each coloured nucleated corpuscle, into two or more secondary corpuscles, the number of which is determined by the number of nuclei developed in the corpuscle previous to its division, and which seldom exceeds two, though it occasionally amounts to three, or, as figured by Fahrner,† even to four; or, secondly, by the formation of two or three smaller corpuscles within each large one, which subsequently dissolves away and liberates its brood. Whichever of these modes of multiplication is pursued, he considers, however, that it is brought to a complete close so soon as the liver is developed. Then, in his opinion, the production of blood-corpuscles is due entirely to this organ, by whose agency an abundant formation of nucleated colourless corpuscles is soon effected, and continues to take place probably through the whole period of embryonic life. The colourless corpuscles thus formed, which are quite different from the colourless embryonic cells found at the first development of the blood, are in all probability converted into coloured blood-corpuscles, either at once, or not until they have multiplied in one or other of the modes just described as happening to the first formed coloured corpuscles. Of the coloured nucleated corpuscles which result from such transformation, the majority flatten, lose their nuclei, and shortly assume all the characters of the ordinary coloured non-nucleated corpuscles found in the blood of Mammalia. The relative quantity of these latter corpuscles increases in proportion to the age of the embryo, so that they soon constitute the principal element of the blood, except of that of the liver, in which, at all periods of embryonic life, colourless and coloured nucleated corpuscles occur in great abundance, owing apparently to the activity of the process of blood-development there taking place.

The latter part, at least, of this account of Kölliker, was fully confirmed by the results of observations made by Mr. Paget, Mr. Malden, and the writer. In a sheep's embryo about four inches and a quarter in length, while the blood of the rest of the body consisted almost entirely of ordinary red non-nucleated corpuscles, that from the liver (obtained from a clot drawn from a section of this organ) contained, besides dark red corpuscles, a large quantity of different-sized, pale, granular, and largely nucleated cells, the characters of which were quite distinct from those of the ordinary liver-cells. Still stronger evidence in favour of this view was obtained from the examination of the blood of a human fœtus at about the commencement of the fifth month of pregnancy. For, while

* Henle und Pfeufer's Zeitschrift, 1846, p. 112, *et seq.*

† De Globulorum Sanguin. in Mammal. Embryon. et adultis origine. Inaug. Diss. 1845.

the blood from the left ventricle of the heart, from the umbilical artery and vena cava superior, was composed principally of ordinary red non-nucleated corpuscles, with a very few pale granular cells, that from the liver and that also—though from this source the characters of the blood were less manifest—from the vena cava inferior just previous to its entrance into the right auricle, contained, besides red non-nucleated corpuscles, a considerable number of ordinary pale corpuscles like lymph-corpuscles, and several larger pale granular corpuscles, with distinct large nuclei. The appearances, indeed, presented by the blood obtained from these two latter sources, but especially from the liver, were just such as would indicate the existence of a process of rapid development of blood-corpuscles. Of this process the several varieties of corpuscles found, probably represented so many stages from the first condition of pale spherical granular nucleated cells, to the coloured, flattened, smooth, non-nucleated corpuscles.*

With regard to the probable mode in which the liver performs this office of developing blood-corpuscles, Kölliker does not offer any decided opinion. He considers that it bears no particular relation to the development of the proper secreting tissue of the organ, for the formation of blood-corpuscles in the liver takes place even before the secretion of bile commences. Professor E. H. Weber,† who also admits the importance of the liver as an organ for the formation of blood in the embryo, at least of birds and frogs, is of opinion that the elements of bile and the corpuscles of blood stand, as it were, in a kind of complemental relation to each other, the separation of the one furnishing the conditions favourable to the development of the other. The seat of formation, however, both of the blood corpuscles and the bile is considered by Weber to be in the network of minute biliary ducts, and not in the blood-vessels. Certain materials (the contents of the yolk-sac in early embryonic life) are abstracted from the latter into the former set of vessels; and from these materials are formed the elements of bile, and the corpuscles of blood: the one are conveyed through the bile ducts to the gall-bladder and intestines, the others make their way into the blood-vessels; but in what manner is by no means clear.

Whatever share may be taken by the liver in the production of blood-corpuscles during embryonic life, the results of the most recent observations on the subject of the development of the blood, especially of those furnished by Kölliker,‡ Mr. Wharton Jones,§ and Fahrner,‖ to the general truth of which the testimony of the writer, from observations above alluded to, may be added, have shewn that, in the blood of the early Mammalian embryo, at least three several kinds of corpuscles are met with.

* And, since the above was written, still further confirmation of the truth of such an opinion has been obtained from additional examinations of the blood of other Mammalian embryos at different ages.

† Henle und Pfeufer's Zeitschrift, l. c. p. 161.

‡ Op. cit.

§ Philosophical Transactions, 1846.

‖ Op. cit.

These are—to enumerate them by the terms adopted by Kölliker, and to place them in the probable order of their development—1. colourless nucleated corpuscles (fig. 25 A); 2. coloured nucleated corpuscles (B and C); and 3. coloured non-nucleated corpuscles. Varieties in size, form, relative numbers, and shades of colour, are observed in these corpuscles,

Fig. 25.*

such as might be expected from the circumstance that they are probably only different transitional stages of development of one kind of corpuscle, and that bodies in all the intermediate states of this transition are commonly met with in the same sample of blood. Without describing these varieties, which may be found detailed at length by Mr. Wharton Jones, and by Kölliker—with whose descriptions the observations of the writer for the most part agree—it will be sufficient to observe here that very little doubt now remains of the correctness of the opinion that the first variety, namely, the pale or colourless nucleated corpuscles (which, according to Kölliker, are developed in the liver) constitute an early stage in the development of the perfect red corpuscles, and that they are gradually transformed, first into the nucleated coloured corpuscles, by assuming colouring matter, and then into the non-nucleated coloured ones, by losing their nucleus and becoming flattened.

The mode in which the nucleus disappears is not clearly determined. Mr. Wharton Jones is of opinion that the nucleus escapes from the cell, and becoming coloured, constitutes the ordinary red non-nucleated corpuscle of mammalian blood. The principal circumstance which he urges in favour of this view is, that, at least in the adult animal, there is an almost exact correspondence in size between the nucleus of the nucleated blood-cell and the non-nucleated red corpuscle; and that in those animals which have small red corpuscles, as the goat, the nucleus of the nucleated cell also is small, whilst in those which have large red corpuscles, as the elephant, the nucleus also is large.

* Fig. 25. Blood corpuscles from a three months' human embryo, magnif. 300 diams. After Kölliker. A. Nucleated colourless corpuscles from the blood of the liver. *a*, a large nucleated corpuscle with a clear fluid and granules in its interior; *b*, a smaller one from which the granules have disappeared; *c*, a pale double-nucleated corpuscle with granules; *d*, a double-nucleated one slightly coloured; *e*, a single-nucleated, slightly coloured corpuscle, from which the granules have disappeared. B. Slightly coloured nucleated blood-corpuscles from the liver; *a*, with two; *b*, with one; c, with three nuclei. C. Dark-coloured nucleated blood-corpuscles from the aorta; *a*, a large one, with a slight depression; *b*, a smaller one; *c*, one viewed laterally; *d*, a smaller one with a constricted nucleus.

The preponderance of nucleated coloured corpuscles in the blood of the very early mammalian embryo, and their gradual diminution in quantity as the fœtus increases in age was noticed by Kölliker. In other observations which the writer made with Mr. Paget on the blood of two embryonic sheep, each about seven lines in length, the truth of this remark was fully confirmed, as also of the fact observed by other physiologists that the blood corpuscles of the fœtus are decidedly larger than those of the adult. In the blood of each of the embryonic sheep by far the majority of the corpuscles were coloured, had a diameter at least twice as large as that of the red corpuscles in the uterine vein of the parent, and were biconvex in form, often somewhat distorted, and Saturn-shaped; the addition of water brought into view nuclei in almost all of them.*

With regard to the development or fresh formation of corpuscles in the blood after the cessation of embryonic life, Kölliker favours the view advocated by the translator of Müller's Physiology,† and adopted by many physiologists, that this is effected by the transformation of the pale corpuscles of the blood, which (developed in the liver during embryonic life, after this period) are identical with the corpuscles found in the lymph and chyle. In this transformation the corpuscles possibly pass through transitional stages somewhat similar to those undergone by the pale corpuscles of the embryonic blood, though, if this be so, the whole process must take place most rapidly, for the occurrence of the stage of coloured nucleated corpuscle is one of extreme rarity, and has never been observed in the blood of the human subject. Mr. Wharton Jones states that he has seen it in the blood of the horse, and of the elephant. Dr. Carpenter,‡ however, and some other physiologists are still of opinion that the red corpuscles do not owe their origin to the pale ones, but that they multiply either by the division of each corpuscle into two, as maintained by Dr. Owen Rees,§ or by its breaking up into six or more segments, each of which becomes a young blood-disc, as described by Dr. Barry.||

* Subsequent examinations of the blood of several embryonic sheep of various sizes with the particulars of which the writer has been kindly furnished by Mr. Paget, would seem to prove a constant resemblance, except in form, between the characters of Mammalian blood at all periods of embryonic life before the disappearance of the branchial fissures, and those of the blood of fish, in which animals the branchial apparatus is persistent. And it would appear that those peculiarities which characterize the blood of Mammalian animals during extra-uterine life are assumed by the fœtus at the time of, or just after, the closure of the branchial fissures.

† Vol. i. page 155.

‡ Principles of Human Physiology, third edition, p. 107.

§ Gulstonian Lectures, Medical Gazette, March, 1845.

|| Phil. Trans. 1840.

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PREFACE.

The present little work contains a series of experiments, the object of which is to ascertain the law according to which the mixture of two liquids, separated by a membrane, takes place. The reader will, I trust, perceive in these researches an effort to attain, experimentally, to a more exact expression of the conditions under which the apparatus of the circulation acquires all the properties of an apparatus of absorption.

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